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MORFOLOGIA DO ESQUELETO APENDICULAR E DAS CINTURAS PEITORAL E PÉLVICA DOS TITANOSAURIDAE (DINOSAURIA:SAUROPODA) DO NEOCRETÁCEO DE MINAS GERAIS, BRASIL

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Morfologia do Esqueleto Apendicular e das Cinturas Peitoral e Pélvica dos Titanosauridae (Dinosauria:Sauropoda) do Neocretáceo de Minas Gerais, Brasil

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O autor gostaria de dedicar o presente trabalho à memória de Llewellyn Ivor Price (1905-1980), o ilustre paleontólogo que coletou o material aqui descrito, e que tanto contribuiu para o implemento do estudo da Paleontologia dos Vertebrados no Brasil.

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RESUMO

MORFOLOGIA DO ESQUELETO APENDICULAR E DAS CINTURAS PEITORAL E PÉLVICA DOS TITANOSAURIDAE (DINOSAURIA, SAUROPODA) DO NEOCRETÁCEO DE MINAS GERAIS, BRASIL

Setenta e dois ossos fossilizados referidos ao clado Titanosauridae (Dinosauria: Sauropoda) são descritos e ilustrados. Os exemplares são procedentes dos depósitos do Cretáceo Superior continental do Brasil (Bacia Bauru), próximos à localidade de Peirópolis, no estado de Minas Gerais. Todos foram coletados, juntamente com vértebras e três cinturas pélvicas, entre os anos de 1947 e 1974, por L.I. Price, que faleceu antes de poder descrevê-los. O material foi recolhido em três localidades principais: "Localidade 1 ou Caieira", "Rodovia" e "Serra da Galga". Os ossos que não puderam ser associados a nenhuma dessas três origens, ou que representam achados isolados, foram registrados como "Cercanias de Peirópolis". O estudo detectou variação morfológica na maioria das categorias de ossos, que foram separadas em 1 (coracóide, úmero, tíbia), 2 (escápula, placa esternal, ulna, fêmur, fíbula), 3 (púbis, ísquio) ou 4 (rádio) morfótipos distintos. Os morfótipos estão distribuídos pelos três principais locais de coleta. De um total de 42 sinapomorfias descritas na literatura, relacionadas exclusivamente a ossos apendiculares e das cinturas peitoral e pélvica, 33 estão presentes no material de Peirópolis. A presença dessas sinapomorfias permitem diagnosticar o material como pertencente a Sauropoda, Titanosauria, Titanosauridae (não-Saltasaurinae). Os ossos de Peirópolis foram preliminarmente comparados com outras espécies de titanossaurídeos do mundo, especialmente da Argentina. Eles apresentam características morfológicas tanto similares quanto próprias em relação a outras espécies.

Palavras-chave: Sauropoda, Titanosauridae, Grupo Bauru, Cretáceo.

ABSTRACT

MORPHOLOGY OF THE APPENDICULAR SKELETON AND OF THE PECTORAL AND PELVIC GIRDLES OF THE TITANOSAURIDAE (DINOSAURIA, SAUROPODA) FROM THE LATE CRETACEOUS OF MINAS GERAIS, BRAZIL

Seventy-two appendicular and girdle bones referred to the family Titanosauridae (Dinosauria: Sauropoda) are described and figured. They have been found in Continental Upper Cretaceous strata of Brazil (Bauru Basin), near the city of Peirópolis, state of Minas Gerais. All of them were collected, together with vertebrae and three pelves, from 1947 to 1974 by L.I. Price, who passed away before he could study them. The material comes from three main sites: "Site 1 or Caieira", "Rodovia", and "Serra da Galga". The bones which are not referable to any of these sites, or are isolated findings, have been scored as Peirópolis surroundings". The study detected morphological variation in most of the bone categories, which were separated into 1 (coracoid, humerus, tibia), 2 (scapula, sternal plate, ulna, femur, fibula), 3 (pubis, ischium) or 4 (radius) distinct morphotypes. The morphotypes are widespread among the three main collecting sites. From a total of 42 possible synapomorphies described in the literature, which are related exclusively to girdle and limb bones, 33 are present in the Peirópolis material. The presence of these synapomorphies diagnose this material as Sauropoda, Titanosauria, Titanosauridae (non-Saltasaurinae). The bones from Peirópolis were preliminary compared with other titanosaurid species of the world, especially from Argentina. They show both similar and unique morphological features in respect to other titanosaurid species.

Key words: Sauropoda, Titanosauridae, Bauru Group, Cretaceous.

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INTRODUÇÃO

A fauna dinossauriana da América do Sul tem sido progressivamente melhor conhecida, graças a sucessivos novos achados fossilíferos, que ocorreram ao longo das duas últimas décadas. Entre esses achados, destacam-se os Saurópodos (dinossauros herbívoros, quadrúpedes, de grande porte) da família Titanosauridae Lydekker, 1885, tanto na Argentina (BONAPARTE, 1996), quanto no Brasil (PRICE, 1951, 1961; KELLNER & CAMPOS, 1997), onde restos do esqueleto apendicular são os achados mais comuns.

No Brasil, os mais importantes estratos que produziram restos de titanossaurídeos pertencem ao grupo Bauru (Bacia Bauru, também chamada de Bacia do Alto Paraná), de idade cretácica, e encontram-se depositados principalmente sobres os estados de São Paulo, Mato Grosso e Minas Gerais (CAMPOS & KELLNER, 1991; KELLNER, 1996; FERNANDES & COIMBRA, 1996).

A mais importante coleção de fósseis de Titanosauridae, no Brasil, foi organizada por Llewellyn Ivor Price (Fig. 1), que coletou uma grande quantidade de ossos nas cercanias da cidade de Peirópolis (Fig. 2), próxima à cidade de Uberaba (Minas Gerais), entre os anos de 1947 e 1974 (AZEVEDO & KELLNER, 1998). Todo o material coletado pertence ao acervo do Museu de Ciências da Terra – MCT, do Departamento Nacional de Produção Mineral do Rio de Janeiro (DNPM/RJ). Exceto por algumas descrições preliminares (POWELL, 1987a; CAMPOS & KELLNER, 1999), a maior parte das peças dessa coleção permanece ainda desconhecida para a Ciência.

Até o presente momento, apenas duas espécies de dinossauros titanossaurídeos foram formalmente descritas no Brasil: *Antarctosaurus brasiliensis* Arid & Vizotto, 1971 e *Gondwanatitan faustoi* Kellner & Azevedo, 1999. Alguns fragmentos ósseos encontrados no estado de São Paulo (Guararapes) foram identificados apenas ao nível de subfamília (LEONARDI & DUSZCZAK, 1977). A coleção do DNPM/RJ, no entanto, é composta por grande quantidade de ossos de titanossaurídeos, em excelente estado de preservação, e já preparados para estudo (KELLNER, 1998). Esse material é composto essencialmente por vértebras (cervicais, dorsais e caudais), bem como por muitos ossos das cinturas peitoral e pélvica e ossos apendiculares.. Apesar da falta de material craniano, o material mencionado é de grande importância para o estudo da morfologia, sistemática e filogenia dos dinossauros saurópodos (SALGADO *et al.*, 1997a; WILSON & SERENO, 1998; SANZ *et al.*, 1999).

Análises cladísticas de Sauropoda resultaram em 17 sinapomorfias para esse clado (WILSON & SERENO, 1998). Considerando-se que o clado Eusauropoda inclui todos os saurópodos conhecidos, com exceção de *Vulcanodon*, esse número é acrescido de mais 40 sinapomorfias, resultando em um total de 57 caracteres possíveis a diagnosticar um membro do clado dos Saurópodos (com exceção de *Vulcanodon*). Dos primeiros 17 caracteres, apenas o caráter nº 2 (número de vértebras sacrais 4 ou mais) não se refere à morfologia do esqueleto apendicular. No nível de Eusauropoda, do total de 40 caracteres, apenas 16 se referem aos ossos dos membros. Acima do nível de Eusauropoda, os caracteres referentes aos ossos apendiculares nunca são a maioria do total de sinapomorfias de cada nível taxonômico. O mesmo acontece em Titanosauridae, onde, de um total de 20 caracteres, apenas 7 se referem ao esqueleto apendicular (SALGADO *et al.*, 1997a).

OBJETIVOS DO PRESENTE TRABALHO

O presente trabalho centra-se em três objetivos principais:

1. Catalogar e identificar o material pertencente a saurópodos, coletado por L.I.Price, registrando-o na Coleção de Vertebrados Fósseis do DNPM/RJ, tentando recobrar a maior quantidade possível de informações de campo referente a este material. Para essa tarefa, confiamos na ajuda de Diógenes de Almeida Campos, um paleontólogo que colaborou com Price no DNPM/RJ, participando de trabalhos de campo, e que tem conhecimento do afloramento de origem de muitos ossos fossilizados provenientes de Peirópolis.

2. Descrever a morfologia dos ossos que compõem o esqueleto apendicular e das cinturas peitoral e pélvica dos titanossaurídeos brasileiros, utilizando o material das coleções do DNPM/RJ e do MN/UFRJ.

3. Verificar, após a análise morfológica prevista no item 2:

a) se existe variação morfológica dentro do material estudado;

b) ocorrendo essa variação, se esta indica uma diversidade faunística entre os locais de coleta;

c) se as sinapomorfias descritas na literatura estão presentes no material brasileiro;

d) se existem características morfológicas que diferenciem o material do Brasil das outras espécies conhecidas de titanossaurídeos, especialmente do próprio Brasil, da Argentina, da América do Norte, da Europa, da África e da Ásia;

e) se é possível detectar variação morfológica dentro dessas características que tenham potencial para utilização futura na construção de hipóteses filogenéticas enfocando os titanossaurídeos.

BREVE REVISÃO DA CLASSIFICAÇÃO DOS SAUROPODA

Desde que Sir Richard Owen criou a ordem Dinosauria, em 1841, baseando-se nas semelhanças apresentadas por três gigantescos répteis extintos encontrados na Grã-Bretanha (OWEN, 1842), nosso conhecimento sobre esses curiosos e espantosos seres vem se ampliando progressivamente até os dias de hoje. Os dinossauros, explorados pela mídia, ultrapassaram as fronteiras da Paleontologia, tornando-se bem conhecidos do público em geral. De todas as ilustrações representando um dinossauro, aquela de um saurópodo – um gigantesco animal quadrúpede, com um longo pescoço provido de uma cabeça risivelmente pequena, comendo placidamente algumas plantas, próximo a um pântano, sacudindo para ambos os lados a sua longa cauda em forma de chicote - deve ser a imagem mais prontamente associada na mente de qualquer pessoa que já tenha se deparado com a palavra "dinossauro".

Os dinossauros saurópodos são tradicionalmente classificados dentro da Ordem Saurischia, juntamente com duas outras subordens: os Theropoda (carnívoros bípedes) e os Prosauropoda (dinossauros herbívoros de médio a grande porte, quadrúpedes facultativos, que floresceram durante o Triássico). Os Prosauropoda são agrupados juntamente com os Sauropoda dentro da subordem Sauropodomorpha, e são considerados como ancestrais dos próprios Sauropoda. Estudos recentes onde foi utilizada análise cladística confirmaram a monofilia dos Saurischia, com uma dicotomia levando aos Theropoda e aos Sauropodomorpha (ex. GAUTHIER, 1986; BENTON, 1990). O posicionamento dos Prosauropoda em relação aos Sauropoda (se estes são um grupo irmão monofilético dos Sauropoda, ou um grupamento parafilético de táxons sucessivos culminando naqueles) ainda é matéria de disputa.

Os dinossauros saurópodos prosperaram principalmente no Jurássico, quando muitas espécies atingiram grande tamanho (ultrapassando 30 metros de comprimento), provavelmente pesando até 80 toneladas. Após os Jurássico, suas populações declinaram no hemisfério norte, sendo progressivamente substituídas por faunas predominantemente compostas por dinossauros herbívoros ornitisquianos. Apesar disso, representantes dos Sauropoda sobreviveram ao sul, no paleocontinente Gondwana, onde prosperaram ao longo do Cretáceo, até a grande extinção que marcou o fim do Mesozóico.

Os dinossauros saurópodos se caracterizam por sua postura quadrúpede obrigatória, presença de pescoço e cauda longos e cabeças comparativamente pequenas em relação ao tamanho do corpo. Esse contraste entre cabeça e corpo faz com que a cabeça se desprenda facilmente do corpo do animal morto. Portanto, os crânios raramente se fossilizam junto ao esqueleto, resultando na perda de importantes informações para o estudo da anatomia dos saurópodos e de suas relações filogenéticas. A lacuna é preenchida em parte pelo estudo detalhado da anatomia vertebral. O grande tamanho atingido por esses animais terrestres, com o conseqüente aumento do peso corporal a ser suportado pelo corpo, exigiu modificações na anatomia de seus esqueletos, e o sistema axial sofreu muitas adaptações a fim de reforçar e tornar mais leves os elementos vertebrais. Os saurópodos, então, desenvolveram uma série de escavações (para diminuição de peso) e lâminas (para reforço ósseo) em suas vértebras, especialmente as cervicais e dorsais. Cada gênero possui uma configuração de características vertebrais diagnósticas próprias, de maneira que o estudo da anatomia vertebral adquiriu papel preponderante na identificação e classificação dos saurópodos (McINTOSH, 1990).

Os saurópodos não viveram em pântanos, como se pensava anteriormente, mas habitaram em terra seca. A evidência icnológica favorece essa interpretação dos saurópodos como animais terrestres. Essa evidência também sugere que os saurópodos eram animais gregários, e que viviam em manadas (DODSON, 1990). Isso é compatível com a idéia de que os saurópodos eram ovíparos, uma vez que alguns ovos fossilizados têm sido encontrados associados a jazigos fossilíferos formados por restos de saurópodos na França e no Brasil. O registro icnológico ainda sugere que, ao caminhar, os saurópodos não arrastavam suas longas caudas, mas as mantinham elevadas acima do solo.

A história dos Sauropoda iniciou-se com O. C. MARSH (1878), que cunhou o nome para uma subordem dos Saurischia, a fim de acomodar dinossauros quadrúpedes de proporções gigantescas, de hábitos herbívoros, providos de pescoços e caudas longos e

vértebras dorsais de morfologia complexa. Inicialmente, Marsh incluiu apenas uma família dentro dos Sauropoda – Atlantosauridae. Conforme novas espécies foram sendo descobertas, Marsh sucessivamente criava novas famílias – como Morosauridae, Diplodocidae e Pleurocoelidae – expandindo o sistema de classificação do grupo original (MARSH, 1895, 1898, *apud* WILSON & SERENO, 1998: 2). Outros autores também contribuíram, adicionando novas famílias ao sistema original de Marsh, ampliando-o ou modificando-o (WILSON & SERENO, 1998: 2).

Um dos autores a contribuir para o estudo dos Sauropoda foi LYDEKKER (1877) que realizou estudos sobre os vertebrados fósseis da Índia, descrevendo então *Titanosaurus indicus*, um dinossauro caracterizado por suas vértebras caudais procélicas incomuns. LYDEKKER (1885) prosseguiu com seus estudos sobre os vertebrados da Índia, propondo então a família Titanosauridae, contribuindo assim com a expansão da classificação dos Sauropoda de Marsh.

Desde então, a família Titanosauridae foi aceita pela maioria dos autores. (HUENE, 1927; 1929). Outros, no entanto, colocavam-na em uma categoria inferior – como a subfamília Titanosaurinae, dentro dos Homalosauropodidae (JANENSCH, 1929). Independentemente da posição taxonômica ocupada pelos Titanosauridae, estes sempre foram considerados filogeneticamente próximos aos Diplodocidae, Apatosauridae e Dicraeosauridae (saurópodos que apresentavam dentes em forma de cavilhas), em oposição às formas que apresentavam dentes em forma de cinzel, representados pelos Camarasauridae e Brachiosauridae, e por muitas algumas formas primitivas coletivamente denominadas de Cetiosauridae (todas estas classificadas como Bothrosauropodidae).

ROMER (1956) elaborou um sistema de classificação em que os Titanosauridae englobavam todas a quatro famílias (agora niveladas à categoria de subfamília) dos Homalosauropodidae. Titanosauridae tornou-se, portanto, um sinônimo de Homalosauropodidae.

O sistema de classificação dos saurópodos proposto por Romer prevaleceu durante as décadas de 60 e 70 do século passado, quando novas descobertas, feitas particularmente na África e na China, associadas ao acúmulo de dados sobre os Sauropoda, levaram a maioria dos autores a aceitar um sistema de classificação mais estável, baseado em seis famílias: Vulcanodontidae, Cetiosauridae, Camarasauridae, Brachiosauridae, Diplodocidae e Titanosauridae (BONAPARTE, 1986; NORMAN, 1985; CARROLL, 1988; BENTON, 1990; McINTOSH, 1990; McINTOSH, BREET-SURMAN & FARLOW, 1997).

Neste novo sistema de classificação, os Vulcanodontidae Cooper, 1984, são representados por uma única espécie – *Vulcanodon caribaensis* Raath, 1972, do limite Triássico-Jurássico do Zimbabwe. Esta espécie é conhecida por um esqueleto incompleto, ao qual falta o crânio. *V. caribaensis* é considerado o saurópodo mais primitivo (McINTOSH, 1990; WILSON & SERENO, 1998).

Os Cetiosauridae Lydekker, 1888 são um grupo de saurópodos generalizados do Jurássico Médio ao Tardio, com ampla distribuição geográfica, nos quais se incluem muitos gêneros, como, por exemplo, *Cetiosaurus* (Inglaterra), *Patagosaurus* (Argentina), *Shunosaurus* (China) e *Haplocanthosaurus* (EUA). Essa família é provavelmente um grupo parafilético, e necessita ser revista.

Os Brachiosauridae Riggs, 1904 são melhor representados pelo gênero *Brachiosaurus*, encontrado no Jurássico Superior da África e dos Estado Unidos da América. Há, no entanto, muitas outras espécies classificadas dentro dessa família, estendendo sua abrangência temporal do Neojurássico ao Eocretáceo (McINTOSH, 1990).
Os Camarasauridae Cope, 1877 são representados apenas pelo bem conhecido gênero *Camarasaurus*, do Jurássico Superior dos Estados Unidos da América (Formação Morrison). Esse gênero tem todas a partes de seu esqueleto bem conhecidas, incluindo o crânio. Um espécime foi encontrado quase que totalmente articulado, tornando *Camarasaurus* o saurópodo melhor conhecido.

Diplodocidae Marsh, 1884 é a família com o maior número de formas bem conhecidas, com muitos esqueletos e crânios descritos. McIntosh (1990) reconhece três subfamílias dentro dos Diplodocidae: Diplodocinae (representada pelos gêneros norte-americanos *Diplodocus*, *Barosaurus*, *Apatosaurus* e *Amphicoelias*); Dicraeosaurinae (representada por *Dicraeosaurus* na África e *Nemegtosaurus* e *Quaesitosaurus* na Mongólia, *Rebbachisaurus* no Marrocos e *Amargasaurus* na Argentina) e Mamenchisaurinae (representada por *Mamenchisaurus*, da China).

Os Diplodocinae e os Mamenchisaurinae estão restritos ao Jurássico Superior; os Dicraeosaurinae foram encontrados no Jurássico Superior (*Dicraeosaurus*) e tanto no Cretáceo Inferior (*Rebbachisaurus*) quanto no Superior (*Nemegtosaurus* e *Quaesitosaurus*).

Os Titanosauridae foram um bem sucedido grupo de saurópodos, com origem provável no Neojurássico, que, sobrevivendo à extinção no fim do Jurássico, prosperou especialmente ao longo do Neocretáceo, espalhando-se através de uma ampla área

geográfica na qual se incluem a Europa, a África, a Ásia, a Austrália e as Américas do Norte e do Sul. Eles se caracterizam, entre muitos fatores, principalmente pelos centros procélicos incomuns de suas vértebras caudais anteriores, que possuem articulações bem desenvolvidas, do tipo "esfera-soquete" ("ball-and-socket").

O sistema de seis famílias não é livre de críticas, sendo continuamente debatido. Várias outras famílias têm sido propostas ou aceitas por alguns autores, que criam os seus próprios sistemas de classificação: Chubutisauridae (CORRO, 1975); Dicraeosauridae (BONAPARTE, 1986); Andesauridae (BONAPARTE, 1996); Euhelopodidae (CARROLL, 1988; UPCHURCH, 1995); Nemegtosauridae (UPCHURCH, 1999) são apenas alguns exemplos.

Com o advento da Sistemática Filogenética (Cladismo), iniciou-se a produção de cladogramas nos quais representava-se as relações filogenéticas dos dinossauros. O trabalho de GAUTHIER (1986) – um clássico – lida com os dinossauros saurisquianos (Theropoda e Sauropoda) e propõe a origem das aves a partir dos dinossauros Theropoda. O trabalho de Gauthier atingiu, imediatamente, duas importantes constatações: primeiro, a percepção de que os Sauropoda podiam ser separados em um grupo de formas primitivas sucessiva (*Vulcanodon* e *Barapasaurus*), em oposição às formas mais derivadas, representadas por quatro das famílias presentes no sistema clássico. Segundo, a distribuição dessas quatro famílias em dois grupos irmãos: os "Camarassauros" (Camarasauridae e Brachiosauridae) e os "Titanossauros" (Diplodocidae e Titanosauridae), comprovando assim a natureza monofilética de cada uma dessas quatro famílias.

O Trabalho de Gauthier foi o precursor de futuras mudanças nas teorias sobre filogenia dos Sauropoda, que se mostrariam resultados de maior impacto ao longo dos anos 90 do último século. Muitos autores publicaram seus importantes estudos sobre a filogenia dos Saurópodos desde então: UPCHURCH (1995); CALVO & SALGADO (1995); SALGADO, CORIA & CALVO (1997a); WILSON & SERENO (1998); SANZ *et al.* (1999). Cada trabalho resultou em seu próprio sistema de classificação, mas dois deles (SALGADO, CORIA & CALVO, 1997a; WILSON & SERENO, 1998) mostraram semelhanças ao esboçarem um novo arranjo das relações filogenéticas das quatro principais famílias de saurópodos, modificando o sistema dicotômico prévio de Gauthier (o qual, na época em que foi proposto, coincidia com o sistema de classificação tradicional).

Os dois trabalhos citados acima concordavam com a análise de Gauthier ao posicionar uma série sucessiva de táxons primitivos (*Vulcanodon*, *Shunosaurus*,

Barapasaurus e *Omeisaurus*), até atingir um clado composto por formas do Neojurássico e Cretáceo – os Neosauropoda (Figs. 3 e 4).

Os Neosauropoda, por sua vez, foram divididos em dois clados irmãos: Diplodocidae (SALGADO *et al.*, 1997a) ou Diplodocoidea (WILSON & SERENO, 1998), em oposição ao grupo irmão formado por todos os saurópodos derivados restantes, denominado Camarasauromorpha (SALGADO *et al.*, 1997a) ou Macronaria (WILSON & SERENO, 1998), os quais incluem o gênero *Haplocanthosaurus* + Camarasauromorpha).

Os Camarasauromorpha são divididos em Camarasauridae (SALGADO *et al.* 1997a) ou apenas *Camarasaurus* (WILSON & SERENO, 1998), e seu grupo irmão – os Titanosauriformes.

Os Titanosauriformes são então divididos em Brachiosauridae (WILSON & SERENO, 1998) ou *Brachiosaurus* (SALGADO *et al.* 1997a) e seu grupo irmão Somphospondyli (*Euhelopus* + Titanosauria na análise de WILSON & SERENO, 1998) ou o Taxon I (SALGADO *et al.*, 1997a – esses autores não incluíram o gênero *Euhelopus* em sua análise).

O sistema de classificação dos Sauropoda baseado nos dois trabalhos acima pode ser resumido como se segue (Figs. 3 e 4):

SAUROPODOMORPHA
- Prosauropoda
- Sauropoda
  - Neosauropoda
    - Diplodocoidea ou Diplodocidae
    - Macronaria
      - *Haplocanthosaurus*
      - Camarasauromorpha ou *Camarasaurus*
        - Titanosauriformes
          - Brachiosauridae
          - Somphospondyli
            - *Euhelopus*
            - Titanosauria

A análise de WILSON & SERENO (1998) vai até os Titanosauria, mas aquela de SALGADO *et al.* (1997a) continua, tentando, assim, esclarecer as relações filogenéticas dos Titanossaurianos. O trabalho de SANZ *et al.* (1999), também lida com relações filogenéticas dos Titanosauridae, e ambos serão comentados adiante.

Os Sauropoda são diagnosticados, tradicionalmente, pelo grande tamanho corporal, crânios relativamente pequenos, pescoços longos, caudas longas, crânio com grandes narinas dorsais, jugal muito reduzido, geralmente excluído da margem ventral do crânio, quadradojugal grande, capacidade endocraniana relativamente pequena, palato muito arqueado, com pterigóides desenvolvidos, centros das vértebras pré-sacrais com profundos pleurocelos e/ou tecido esponjoso (para diminuição do peso), arcos neurais e espinhas muito reduzidas a um conjunto de lâminas complexas, 12 a 19 vértebras cervicais, 8 a 14 dorsais, escápula orientada mais horizontalmente do que verticalmente, ílio com um processo pré-acetabular muito alargado, e com o pedúnculo púbico mais longo do que o isquiádico, ossos dos membros robustos e sólidos, ausência de cavidade entre o grande trocânter e a cabeça do fêmur, carpo e tarso reduzidos a um ou dois elementos cada, menos, talvez, nas formas mais primitivas, metacarpais mais longos do que os metatarsais, antigas, redução do número de falanges na mão, dedo I é o único a reter uma garra, número de falanges reduzido nos dedos IV e V do pé (MCINTOSH, 1990).

Uma lista de sinapomorfias que definem os Sauropoda incluem os seguintes caracteres (WILSON & SERENO, 1998):

1. Postura quadrúpede obrigatória, com membros colunares e metapodiais curtos.
2. Quatro ou mais vértebras sacrais.
3. Crista deltopeitoral do úmero baixa.
4. Olécrano reduzido ou ausente.
5. Extremidade proximal da ulna trirradiada, com fossa radial profunda.
6. Côndilo distal radial subrretangular com margem posterior plana para a ulna.
7. Ílio com pedúnculo isquiádico reduzido
8. Diáfise do isquio igual ou mais longa do que a diáfise púbica
9. Diáfise do isquio com extremidade distal plana dorsoventralmente
10. Corpo do fêmur transversalmente elíptico, eixo mais longo da elipse orientado mediolateralmente.

11. 4º trocânter do fêmur desenvolvido como uma crista baixa.

12. Fossa e forames astragalares na base do processo ascendente ausentes.

13. Tarsais distais 3 e 4 ausentes ou não ossificados.

14. Metatarsais I e V com extremidades proximais subiguais em área aos metatarsais II e IV.

15. Comprimento do metatarsal V pelo menos 70% daquele do metatarsal IV.

16. Dígito pedal I com ungual aumentado.

17. Ungual do dígito pedal I alto e estreito (forma de foice).

Uma lista de sinapomorfias dos Eusauropoda continua da seguinte forma (WILSON & SERENO, 1998):

18. Narinas externas retraídas posterodorsalmente

19. margem anterior do focinho chanfrada

20. Fossa ântero-orbital ausente

21. Borda maxilar da narina longa

22. Processo anterior do pré-frontal ausente

23. Contato entre esquamosal-quadradojugal ausente

24. Ramo anterior do quadradojugal alongado, expandido distalmente

25. Região infra-orbital do crânio ântero-posteriormente curta

26. Região supratemporal do crânio ântero-posteriormente curta

27. Fossa supratemporal lateralmente exposta

28. Quadrado com fossa posterior alongada

29. Ramo lateral do palatino estreito

30. Ramo do dentário: altura máxima da extremidade anterior aproximadamente 150% da menor altura do ramo

31. Linhas dentárias amplamente arqueadas anteriormente

32. Coroas espatuladas

33. Esmalte dentário com textura enrugada

34. Sobreposição das coroas dentárias

35. Oclusão coroa a coroa precisa

36. área dentária de desgaste em forma de V (oclusão interdigitada)

37. 13 ou mais vértebras cervicais

38. Centros cervicais opistocélicos

39. Arcos neurais das cervicais médias altos, maiores que o diâmetro do centro vertebral

40. Espinhas neurais dorsais mais largas transversalmente do que ântero-posteriormente

41. arcos hemais distais (chevrons) com projeções anteriores e posteriores

42. Carpais em forma de bloco.

43. Falanges manuais dos dígitos II e III reduzidas (II - ungual, III- 3 e ungual ausentes, fórmula digital 2-2-2-2-2 ou menos)

44. Falanges manuais (que não os unguais) mais largas que longas.

45. Lâmina ilíaca com margem dorsal semicircular e processo pré-acetabular desenvolvido

46. Diáfise distal do púbis torcida póstero-medialmente

47. Crista cnemial da tíbia projetando-se lateralmente.

48. Processo póstero-ventral da tíbia reduzido.

49. Trocânter lateral fibular.

50. Metatarsal III com 25% ou menos do comprimento da tíbia.

51. Menor largura do corpo do metatarsal I maior do que o dos metatarsais II-IV.

52. Metatarsais com configuração espalhada.

53. Falanges pedais (que não os unguais) curtas.

54. Ungual do dedo pedal I igual ou mais longo que o metatarsal I.

55. Dígitos pedais II-IV com penúltimas falanges rudimentares ou ausentes.

56. Dígitos pedais II e III com unguais falciformes.

57. Ungual do dígito pedal IV rudimentar ou ausente.

Acima deste nível, os Sauropoda são divididos em alguns outros subgrupos. Um sistema de classificação completo dos Sauropoda, com as respectivas sinapomorfias, é apresentado no apêndice.

BREVE REVISÃO DA CLASSIFICAÇÃO DOS TITANOSAURIDAE

A história dos Titanosauridae inicia-se com LYDEKKER (1877). Esse autor complementou um trabalho sobre os vertebrados fósseis da Índia, no qual descreveu *Titanosaurus indicus*, um dinossauros saurópodo caracterizado por suas vértebras caudais

procélicas incomuns. Lydekker continuou a estudar os vertebrados da Índia, descrevendo outra espécie do gênero *Titanosaurus* – *T. blanfordi* (LYDEKKER, 1879). Essas descobertas levaram-no a propor o nome Titanosauridae para acomodar aqueles dinossauros saurópodos com características próprias em suas vértebras caudais (LYDEKKER, 1885). As contribuições de Lydekker aos Titanosauridae se estenderiam ao estrangeiro, uma vez que, durante uma visita à Argentina, estudou e descobriu novos materiais de dinossauros, identificando-os também como titanossaurídeos, ampliando assim a distribuição geográfica daquela família da Índia para a América do Sul (LYDEKKER, 1893). Em seu trabalho, Lydekker descreveu uma nova espécie do gênero *Titanosaurus* – *T. australis*, baseando-se em uma grande coleção de séries de vértebras e ossos isolados de membros; assim como um novo gênero e espécie, *Argyrosaurus superbus*, baseando-se no esqueleto articulado de um grande membro anterior, incluindo os metacarpais.

DEPERET (1896) identificou duas vértebras caudais provenientes de Madagascar as uma nova espécie de *Titanosaurus*, batizando-a de *T. madagascariensis*. Um osso dérmico foi encontrado juntamente com os restos desse animal, levando Deperet a sugerir que os Titanosauridae teriam o corpo protegido por uma armadura óssea.

Hypselosaurus priscus Matheron, 1869 (restos isolados de pós-crânio de pelo menos 10 indivíduos) e *Macrurosaurus semnus* Seeley, 1869 (seqüência de vértebras caudais) são outras descobertas do século XIX que só mais tarde foram identificadas como membros dos Titanosauridae, provando que representantes dessa família prosperaram durante o Cretáceo Europeu.

O início do século XX foi especialmente proveitoso em se tratando de achados de materiais relacionados aos Titanosauridae.

STERNFELD (1911) estudou *Gigantosaurus robustus* Fraas, 1908 – um grande saurópodo encontrado nos depósitos de Tendaguru (jurássico Superior da Tanzânia), e estabeleceu um novo gênero - *Tornieria*, substituindo *Gigantosaurus*, o qual já se encontrava ocupado (JACOBS *et al.* 1993). *Tornieria* é, portanto, o mais antigo titanossaurídeo conhecido, embora problemático, pois alguns dos materiais originais (especialmente ossos dos membros) podem não ter pertencido a ele (McINTOSH, 1990: 397).

HUENE (1927) examinou alguns materiais do Neocretáceo da região de Colina (São Paulo) e identificou um vértebra caudal como pertencente a um dinossauro do gênero

Titanosaurus, possivelmente *T. australis*, sendo este o primeiro registro de um titanossaurídeo no Brasil (CAMPOS & KELLNER, 1999: 143).

HUENE (1929) seguiu os passos de Lydekker e foi à Argentina, a fim de estudar uma grande quantidade de material dinossauriano coletado por Wichmann e seus colaboradores através daquele país. Ao fim de sua empresa, Huene havia produzido uma enorme monografia, onde ele descreveu e ilustrou em detalhe, não apenas o material previamente analisado por Lydekker, mas também quatro novas espécies de titanossaurídeos: *Titanosaurus robustus*, *Laplatasaurus araukanicus* e os gigantescos *Antarctosaurus wichmannianus* e *Antarctosaurus giganteus*.

Na década seguinte, HUENE (1932) revisou a espécie oriunda da Romênia, *Titanosaurus dacus*, que havia sido previamente descrita por NOPCSA (1915), e a transferiu para um novo gênero - *Magyarosaurus*, descrevendo também duas novas espécies: *M. transylvanicus* e *M. hungaricus*.

No mesmo ano, STROMER (1932) descreveu uma outra espécie, *Aegyptosaurus baharijensis*, que havia sido descoberta durante uma expedição ao deserto do Saara, no Egito. A descoberta de *Aegyptosaurus* estendeu o limite geográfico dos até o continente Africano. Infelizmente, essa espécie foi destruída durante a Segunda Grande Guerra.

GILMORE (1922) reportou uma nova espécie de saurópodo do Cretáceo Superior do Novo México (EUA), baseando-se em um escápula esquerda, que foi denominada *Alamosaurus sanjuanensis*. O reconhecimento dessa espécie como sendo um membro dos Titanosauridae só foi possível em 1946, com a descoberta de um esqueleto incompleto articulado de *Alamosaurus* (GILMORE, 1946). Este espécime possuía um membro anterior totalmente articulado, incluindo a mão, mais uma escápula fundida ao coracóide, ambas as placas esternais (que haviam se fossilizado articuladamente), o sacro (que foi abandonado no campo), um par de ísquios e uma série de 30 vértebras caudais articuladas. A quantidade de material tornaram *A. sanjuanensis* o mais completo e melhor conhecido representante dos titanossaurídeos. Além disso, sua descoberta mostrou que a família Titanosauridae sobreviveu no Cretáceo norte-americano, onde restos de saurópodos eram comuns apenas em depósitos jurássicos.

SWINTON (1947) reportou acerca de novos materiais de *Titanosaurus indicus*.

No Brasil, L.I. Price e seus colaboradores coletaram uma grande quantidade de ossos fossilizados de titanossaurídeos, entre as décadas de quarenta e setenta (PRICE, 1961; CAMPOS & KELLNER, 1999). As descobertas foram feitas no Estado de Minas

Gerais, principalmente nas proximidades da cidade de Uberaba, e registraram muitos afloramentos ricos em restos de titanossaurídeos, incluindo alguns ovos fossilizados (PRICE, 1951). Price organizou uma grande coleção de vertebrados fósseis no setor de Paleontologia do Departamento Nacional de Produção Mineral do Rio de Janeiro, (DNPM/RJ), mas faleceu antes de poder estudar o material e de publicar suas descobertas. Mais detalhes sobre esses achados serão reportados mais adiante.

Embora Price nunca tenha descrito os materiais da coleção do DNPM/RJ, outros achados envolvendo titanossaurídeos foram reportados no Brasil por alguns autores. ARID & VIZOTTO (1971) descreveram uma nova espécie de titanossaurídeo, a qual batizaram de *Antarctosaurus brasiliensis*, baseando-se apenas em poucos restos encontrados em São José do Rio Preto (São Paulo). LEONARDI & DUSZCZAK (1977) reportaram alguns restos fragmentários provenientes de Guararapes (São Paulo), que foram por eles relacionados a um titanossaurídeo da subfamília dos titanossauríneos. Dez anos depois, uma equipe do Museu Nacional do Rio de Janeiro (MN/UFRJ) coletou um esqueleto mais completo no município de Álvarez Machado (São Paulo) (CUNHA, RÊGO & CAPILLA, 1987).

O ritmo dos achados envolvendo titanossaurídeos declinou ao longo dos anos 70, acompanhando uma diminuição do interesse pelo estudo de dinossauros em geral. A situação mudou a partir dos anos 80 com movimento chamado de "dinosaur renaissance" promovido por BAKKER (1975), OSTROM (1979), e outros autores.

Na América do Sul, a retomada dos estudos sobre dinossauros iniciou-se naquela década com uma série de descobertas espetaculares feitas por José Bonaparte e seus colaboradores, na Argentina.

POWELL (1979) revisou os restos de alguns saurópodos provenientes do Cretáceo Superior da província de Salta (Argentina). Entre os materiais, havia restos de um saurópodo que Powell associou ao gênero *Laplatasaurus*. Este saurópodo havia sido previamente identificado como um espécime de *Antarctosaurus* (BONAPARTE & BOSSI, 1967).

BONAPARTE & POWELL (1980) descreveram o restos de um novo titanossaurídeo - *Saltasaurus loricatus* - o mais completo titanossaurídeo descoberto até aquela data. O material era composto por muitas peças ósseas de todas as partes do esqueleto, englobando pelo menos 5 indivíduos. Havia também fragmentos cranianos. A característica mais marcante de *Saltasaurus loricatus* era a presença de um mosaico de

placas dérmicas, que, em vida, cobririam o corpo do animal, confirmando assim o que fora sugerido por Deperet.

POWELL (1986) elaborou uma revisão dos titanossaurídeos da América do Sul. O trabalho foi apresentado como uma tese de doutorado. Infelizmente, os resultados dessa tese não foram ainda publicados. Nessa tese, Powell revisou os gêneros e espécies descritos por Lydekker e Huene, descrevendo novos, como *Aelosaurus*, *Neuquensaurus* (= *Titanosaurus*).

POWELL (1987b) publicou uma descrição breve de *Aelosaurus rionegrinus*, um titanossaurídeo com vértebras caudais típicas. Ele também visitou a coleção de vertebrados fósseis do DNPM/RJ e produziu a primeira descrição preliminar das vértebras dos titanossaurídeos brasileiros que haviam sido coletados por Price. Essas vértebras distribuíam-se entre tipos cervicais, dorsais e caudais, e foram agrupadas em três séries, conhecidas como séries "A", "B" e "C" (POWELL, 1987a).

POWELL (1990) publicou uma descrição preliminar de *Epachthosaurus sciuttoi*, da Patagônia e, dois anos depois, publicou um trabalho detalhado sobre a anatomia de *Saltasaurus loricatus* (POWELL, 1992)

Os estudos sobre os titanossaurídeos da Argentina acelerou-se durante os anos 90, quando uma segunda geração de pesquisadores começou a contribuir com suas próprias descobertas.

CALVO & BONAPARTE (1991) descreveram *Andesaurus delgadoi*, do Albiano-Cenomaniano de Neuquén.

SALGADO & CORIA (1993a) reportaram novos materiais referidos ao gênero *Aelosaurus*, da Formação Allen da província de Rio Negro. No mesmo ano, BONAPARTE & CORIA (1993) descreveram um titanossaurídeo gigantesco achado em Neuquén – *Argentinosaurus huinculensis*, cujas vértebras dorsais chegavam a mais de um metro de altura.

Ainda naquele ano, SALGADO (1993) publicou um trabalho onde revisava a posição sistemática de *Chubutisaurus insignis* Corro, 1975 (que havia sido previamente referido às famílias Chubutisauridae e Brachiosauridae), posicionando-o dentro dos Titanosauridae. Juntamente com Coria (SALGADO & CORIA, 1993b), esse autor estabeleceu a mesma relação para o enigmático *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka, 1977, do Cretáceo Superior da Mongólia. Na descrição original de Borsuk-Bialynicka, esse saurópodo havia sido considerado como um membro dos Camarasauridae,

enquanto todas as afinidades com os titanossaurídeos eram descartadas devido às vértebras caudais de *Opisthocoelicaudia* carecerem da condição procélica típica dos Titanosauridae (essas vértebras são, na verdade, opistocélicas – condição exatamente oposta à encontrada em titanossaurídeos). SALGADO & CORIA (1993b) listaram 16 caracteres derivados compartilhados por *Opisthocoelicaudia* e pelos Titanosauridae, e consideraram a opistocelia das caudais como uma autapomorfia da espécie asiática.

BONAPARTE (1996) publicou uma compilação sobre a Paleontologia de Vertebrados da América do Sul, resumindo as informações disponíveis acerca dos saurópodos argentinos até aquela data.

SALGADO (1996) descreveu uma nova espécie – *Pellegrinisaurus powelli*, baseando-se em uma série de 26 vértebras caudais incompletas.

SALGADO, CORIA & CALVO (1997b) descreveram um terceiro espécime de *Aelosaurus*, da Formação Los Alamitos (província de Rio Negro).

No mesmo ano, esses três autores deram uma grande contribuição ao estudo filogenético dos Titanosauridae, publicando uma análise filogenética baseada em material pós-craniano (SALGADO, CORIA & CALVO, 1997a) (Fig. 4). Os resultados até Titanosauriformes foram mostrados na seção anterior. Seguem-se os resultados encontrados acima dos Titanosauriformes:

Titanosauriformes
- *Brachiosaurus brancai*
- Táxon I
  - *Chubutisaurus insignis*
  - Titanosauria
    - *Andesaurus delgadoi*
    - Titanosauridae
      - *Epachthosaurus sciuttoi* + *Malawisaurus dixeyi*
      - Táxon II
        - Táxon III
          - *Argentinosaurus huinculensis*
          - Táxon IV
            - *Opisthocoelicaudia skarzynskii*
            - Titanosaurinae DGM "B" Series.
        - Táxon V
          - *Aelosaurus*
          - Táxon VI
            - *Alamosaurus sanjuanensis*
            - Saltasaurinae
              - *Neuquensaurus australis*
              - *Saltasaurus loricatus*

Os anos 90 também foram profícuos em trabalhos sobre os Titanosauridae de outros continentes:

JACOBS, WINKLER, DOWNS & GOMANI (1993) publicaram um trabalho sobre novos materiais de um titanossaurídeo do Eocretáceo de Malawi (África), *Tornieria dixeyi*, transferindo-o para um novo gênero, *Malawisaurus*.

LE LOEUFF (1995) reportou em descreveu brevemente *Ampelosaurus atacis*, um novo titanossaurídeo do Cretáceo Superior da França. A descrição detalhada dessa espécie ainda está sendo executada por Le Loeuff. *Ampelosaurus atacis* é representado por uma grande quantidade de materiais, incluindo dentes, vértebras dorsais e caudais, ossos das cinturas e membros e osteodermos.

JAIN & BANDYOPADHYAY (1997) descreveram uma espécie nova de *Titanosaurus*, quase completa (sem crânio), proveniente do Cretáceo Superior da Índia, denominada *T. colberti*.

WILSON, MARTINEZ & ALCOBER (1999) descreveram, pela primeira vez, um segmento caudal distal de um titanossaurídeo do Cretáceo Superior de Mendoza (Argentina).

No mesmo ano, KELLNER & AZEVEDO (1999) descreveram a segunda espécie de titanossaurídeo do Brasil: *Gondwanatitan faustoi*. Esse espécime é o mesmo que havia sido coletado em 1987 em Álvares Machado (São Paulo).

Ainda em 1999, foi publicado o segundo estudo envolvendo o material coletado por Price. CAMPOS & KELLNER (1999) descreveram três cinturas pélvicas de titanossaurídeos pertencentes ao acervo do DNPM/RJ, e concluíram que estas devem ter pertencido a três espécies diferentes de titanossaurídeos. Esse autores, no entanto, abstiveram-se de dar nomes específicos formais a esses materiais.

SANZ *et al*. (1999) descreveram uma nova espécie de titanossaurídeo proveniente do Cretáceo Superior da Espanha: *Lirainosaurus astibiae*. No mesmo trabalho, foi publicado um cladograma que tentava estabelecer a posição filogenética de *L. astibiae* em relação a outros titanossaurídeos (Fig. 5).

BONAPARTE (1999) publicou um importante trabalho sobre vértebras pré-sacrais dos Sauropodomorpha, incluindo também uma extensa análise das vértebras pré-sacrais dos Titanosauridae.

SALGADO & AZPILICUETA (2000) descreveram uma nova espécie de titanossaurídeo da Argentina - *Rocasaurus muniozi*, incluindo-o entre os Saltasaurinae. No

momento, outro novo titanossaurídeo está sendo estudado na Argentina (CALVO, 2001, comunicação pessoal) e um novo espécime brasileiro, proveniente da Região do Prata (Minas Gerais) está sendo preparado para estudo pela equipe do Museu Nacional (Rio de Janeiro).

Espera-se que o estudo desses novos espécimes, aliado às contribuições do presente trabalho, aumentarão o conhecimento atual acerca dos titanossaurídeos sul-americanos, auxiliando-nos a esclarecer suas relações filogenéticas.

Uma melhor compreensão das relações evolutivas dos titanossaurídeos resta prejudicada pela falta de crânios. Os estudos sistemáticos procedidos até o momento baseiam-se principalmente em caracteres vertebrais das vértebras dorsais e, particularmente, das vértebras caudais.

Uma diagnose tradicional dos Titanosauridae é como se segue: vértebras dorsais com pleurocelos irregulares e espinhas dirigidas posteriormente, processos transversos direcionados dorsalmente e lateralmente, muito robustos na região das espáduas, presença de uma segunda vértebra dorso-sacral cujas costelas encontram-se fundidas ao ílio, caudais fortemente procélicas, com uma proeminência esférica na extremidade distal dos centros vertebrais, ao longo de toda a cauda, arcos neurais caudais posicionados sobre a metade anterior dos respectivos centros vertebrais, placas esternais grandes, processo pré-acetabular do ílio curvado externamente e tornando-se quase horizontal (MCINTOSH, 1990: 394).

Uma lista de sinapomorfias dos Titanosauridae segue abaixo (SALGADO *et. al.*, 1997a):

1. Seis vértebras sacrais
2. Garra do dedo I da mão ausente
3. Vértebras caudais fortemente procélicas
4. Ausência de articulação hiposfeno-hipantro nas vértebras dorsais
5. Placas esternais com formato semilunar
6. Ausência de falanges na mão
7. Lobo pré-acetabular do ílio quase horizontal, projetado externamente

Outras sinapomorfias presentes nos Titanosauridae (exceto em *Epachthosaurus sciuttoi* e *Malawisaurus dixeyi*) são (SALGADO, *et al.*: 1997a):

1. Lâmina pré-espinhal medial desenvolve-se até a base da espinha neural nas vértebras dorsais posteriores

2. Coracóides quadrangulares

Acima deste nível, os Titanosauridae se subdividem em vários outros grupos. Uma classificação completa dos Titanosauridae, acompanhada da respectiva lista de sinapomorfias, é dada no apêndice.

HISTÓRICO DO MATERIAL ESTUDADO

O material fóssil que está sendo estudado no presente trabalho foi coletado por L.I. Price durante as décadas de 40 até 70. Price efetuou importantes trabalhos de campo nas cercanias de Uberaba (Minas Gerais). Peirópolis é uma cidadela localizada próximo a Uberaba. Nessa localidade Price escavou e recolheu a mais importante coleção de material dinossauriano do Brasil, guardando-a no Setor de Paleontologia do Departamento Nacional de Produção Mineral do Rio de Janeiro (DNPM/RJ), sendo esse o órgão governamental onde Price trabalhava. Juntamente com seus colaboradores, Price extraiu e preparou centenas de ossos de vários afloramentos em torno de Peirópolis. O material era excelente, tanto em qualidade quanto quantidade. Price planejava descrever todo o material em uma grande monografia sobre os titanossaurídeos brasileiros, mas faleceu repentinamente antes disso (CAMPOS & KELLNER, 1999). Após o inesperado passamento de Price, o material de Peirópolis ficou abandonado, não tendo sido nem catalogado, nem incluído na coleção de vertebrados fósseis do DNPM/RJ.

Algumas seqüências de vértebras receberam apenas descrição preliminar (POWELL, 1987a). Além disso, três pelves quase completas foram recentemente descritas, tendo sido sugerido que cada uma delas pertenceria a uma espécie diferente (CAMPOS & KELLNER, 1999). Todos os outros ossos, referentes principalmente ao esqueleto apendicular, permaneciam ainda não descritos.

O material em estudo é proveniente de três jazigos fossilíferos principais de Peirópolis: Localidade 1 ou Caieira, Rodovia e Serra da Galga (seguindo-se a terminologia de Price, descrita em CAMPOS & KELLNER, 1999). Infelizmente, as anotações de

campo de Price perderam-se após sua morte, privando-nos de valiosas informações acerca desses três jazigos.

O melhor material foi extraído da Localidade 1 (Fig. 6). Este é o único local de coleta registrado em mapa de campo (CAMPOS & KELLNER, 1999). O sítio de Serra da Galga produziu restos interessantes, e o sítio Rodovia contribuiu apenas com poucos ossos.

PANORAMA GEOLÓGICO

A Bacia do Paraná é uma área deposicional extensa (cerca de 1.600.000 km^2), que cobre quatro países sul-americanos: Brasil, Paraguai, Uruguai e Argentina. No Brasil, seus sedimentos cobrem os estados de São Paulo, Paraná, Santa Catarina, Rio Grande do Sul, Mato Grosso, Mato Grosso do Sul e Goiás, perfazendo uma área de 1.000.000 km^2.
Os depósitos variam em idade do Paleozóico (Devoniano ao Permiano) ao Mesozóico (principalmente Triássico e Cretáceo).

Os material fóssil que está sendo estudado no presente trabalho é proveniente de depósitos sedimentares localizados nas proximidades das cidades de Uberaba e Peirópolis, principalmente (Minas Gerais). Esses sedimentos estão depositados na área da Bacia Bauru (ou Bacia do Alto-Paraná), uma entidade sedimentar que era considerada anteriormente como parte integrante de uma bacia de maior extensão – a Bacia do Paraná (Fig. 7).

A Bacia do Paraná é limitada e dividida por uma série de importantes arcos estruturais, o que levou sua subdivisão em cinco sub-bacias: a) Alto Paraná; b) Paranaense-Catarinense; c) Uruguaia-Sul-rio-grandense; d) Chaco-Paraná e e) Ocidental (PETRI & FÚLFARO, 1983).

A sub-bacia do Alto Paraná compreende os estados de São Paulo, Minas Gerais (onde se encontram as cidade de Uberaba e Peirópolis) e Goiás. Recentemente, as peculiaridades geológicas dessa sub-bacia levou alguns autores a considerá-la uma bacia independente, denominando-a Bacia Bauru (FERNANDES & COIMBRA, 1996).

A bacia Bauru é uma depressão que se desenvolveu no centro sul da Plataforma Sul-americana através de subsidência termo-mecânica durante o Cretáceo tardio, em seguida à ruptura do Gondwana e o surgimento do Oceano Atlântico.
A Bacia Bauru se espalha por uma área de 370.000 km^2, cobrindo os estados de São Paulo, Parana, Mato Grosso do Sul, Minas Gerais e Goiás. A seqüência sedimentar apresenta espessura de cerca de 300 metros.

A seqüência correspondente ao Cretáceo superior é formada por dois grupos crono-correlatos: Caiuá e Bauru (Fig. 8). Ambos apresentam contato discordante com os depósitos basálticos subjacentes da Formação Serra Geral. São compostos por uma seqüência contínua de rochas continentais siliciclásticas, localmente associadas a rochas vulcânicas, intercaladas por rochas efusivas alcalinas (analcimitos Taiúva).

O grupo Caiuá compõe-se de três formações: Santo Anastácio, Rio Paraná e Goio Erê. Sua descrição não tem importância no presente trabalho.

O grupo Bauru (origem do material fóssil em estudo) compõe-se também de três formações: Adamantina, Uberaba e Marília. Esse grupo é formado por depósitos fluviais e de leques aluviais. O conteúdo fossilífero das formações Adamantina e Marília indica idade Santoniana-Maastrichtiana (FERNANDES & COIMBRA, 1996: 197). Alguns autores reconhecem a Formação Araçatuba, cujos afloramentos localizam-se no Estado de São Paulo, como sendo uma seqüência inferior da Formação Adamantina, atribuindo-lhe idade Campaniana-Maastrichtiana, com base em fósseis de ostrácodos (GOBBO-RODRIGUES, PETRI & BERTINI, 1999).

A Formação Adamantina é composta por arenitos finos, com inclusões ocasionais de matriz carbonática. Seu conteúdo fossilífero compreende peixes, répteis, moluscos, crustáceos e algas. O ambiente tem sido interpretado como um sistema fluvial de rios entrelaçados com lagoas e dunas eólicas.

A Formação Uberaba é composta por arenitos, siltitos e lamitos, mais conglomerados basais com matriz carbonática. O conteúdo fossilífero é muito pobre (fragmentos de ossos), mas alguns ovos têm sido encontrados. O ambiente é interpretado como um sistema fluvial de rios entrelaçados e lagoas, associadas a leques aluviais basais.

A Formação Marília é composta por conglomerados e arenitos finos, com concreções carbonáticas, em matriz carbonática. As estruturas sedimentares mais freqüentes são laminações cruzadas de pequeno a médio porte. O pacote sedimentar alcança 180 metros, e o ambiente deposicional tem sido interpretado como um sistema de rios entrelaçados com leques aluviais. A Formação Marília é rica em fósseis, principalmente peixes, anfíbios e répteis (quelônios, crocodilomorfos e dinossauros), ostrácodos e bivalves (FERNANDES & COIMBRA, 1996; BERTINI *et al.*, 1993).

MATERIAL FÓSSIL E METODOLOGIA

Material fóssil: conjunto de 72 ossos apendiculares e de cinturas peitoral e pélvica da Coleção de Vertebrados Fósseis do Departamento Nacional de Produção Mineral do Rio de Janeiro (DNPM/RJ).

Metodologia:

O presente estudo foi desenvolvido em três fases. Cada fase corresponde a um dos três objetivos citados acima.

Fase 1: CATALOGAÇÃO E IDENTIFICAÇÃO DOS OSSOS FOSSILIZADOS

Esta fase foi subdividida em duas subfases: a) atividades curatoriais e b) classificação e identificação do material.

a) atividades curatoriais: numeração sistemática do material fóssil, catalogando os ossos fósseis da Coleção de Paleontologia de Vertebrados do Departamento Nacional de Produção Mineral do Rio de Janeiro (DNPM/RJ).

b) classificação do material: os ossos fossilizados foram classificados por localidade de origem e identificados, sendo então distribuídos em categorias morfológicas comparáveis, a saber: escápulas, coracóides, placas esternais, úmeros, ulnas, rádios, púbis, isquios, fêmures, tíbias, fíbulas e metapodiais.

Fase 2: DESCRIÇÃO E ILUSTRAÇÃO

Esta fase também foi dividida em duas subfases: a) descrição morfológica e b) ilustração dos ossos.

a) descrição morfológica: os ossos foram estudados categoria por categoria, e sua morfologia foi descrita. Os dados morfológicos foram comparados com os de outros titanossaurídeos já descritos. As comparações foram feitas principalmente através da consulta bibliográfica e, também, suplementada por algumas observações feitas *in loco* durante visitas a algumas instituições de pesquisa estrangeiras. Durante essas visitas,

produziu-se abundante material fotográfico (cerca de 700 fotos), que foi utilizado nos procedimentos comparativos. As seguintes instituições estrangeiras foram visitadas durante a elaboração do presente estudo:

American Museum of Natural History (Nova Iorque – EUA)

Museo de Ciencias Naturales Bernardino Rivadavia (Buenos Aires – Argentina)

Museo de La Plata (La Plata, Buenos Aires – Argentina)

Museo de Geología y Paleontología, Universidad Nacional de Comahue (Neuquén – Argentina)

Museo Provincial de Cipolletti Carlos Ameghino (Cipolletti, Río Negro – Argentina)

Museo Municipal Ernesto Bachmann (Villa El Chocón, Neuquén – Argentina)

As espécies que foram utilizadas nas comparações morfológicas estão listadas no apêndice, assim como as abreviaturas das instituições científicas onde estão depositadas. As Tabelas 13 e 14 apresentam um resumo do material apendicular de titanossaurídeos disponível para comparações.

b) ilustração do material: todos os ossos que compõe o material de estudo foram fotografados por uma câmara convencional (Cannon EOS – modelo Elan IIe). Todas as fotos foram feitas em preto e branco, utilizando-se luz de flash ou iluminação lateral/obliqua (nesse caso, providenciada por uma lâmpada de 500 watts G.E. Photoflood). A iluminação lateral foi empregada para realçar as características morfológicas mais importantes dos ossos estudados.

As fotos foram escaneadas em um scanner marca Minipa, e digitalizadas através do programa Imaging para Windows Millenium. As imagens digitais foram trabalhadas no programa Paintbrush, a fim de se comporem as lâminas.

As figuras referentes à morfologia foram feitas a nanquim, com base nas fotografias. Os desenhos são esquemáticos, e seu propósito é mostrar as características morfológicas das categorias ósseas descritas no texto. Uma lista de abreviaturas anatômicas encontra-se no apêndice.

As figuras foram escaneadas e editadas em programa Adobe Photoshop 6.0.

Ao longo do texto, foram mencionadas figuras e lâminas de trabalhos de outros autores. Para evitar confusão entre aquelas ilustrações e as do presente trabalho, as primeiras foram mencionadas sempre em minúsculas (ex. fig., pl.), e as nossas em maiúsculas (ex. Fig.). A barra de escala, em todas as figuras, é de 10 centímetros.

Fase 3: DISCUSSÃO

Nessa fase foram analisados e discutidos os resultados, tentando responder às questões levantadas no objetivo 3 (itens a, b, c, d, e).

O Presente trabalho está sendo apresentado sob forma de Periódico. O padrão utilizado (com exceção das lâminas fotográficas) obedece às normas de publicação do periódico "Publicações Avulsas do Museu Nacional".

MORPHOLOGY OF THE APPENDICULAR SKELETON AND OF THE PECTORAL AND PELVIC GIRDLES OF THE TITANOSAURIDAE (DINOSAURIA, SAUROPODA) FROM THE LATE CRETACEOUS OF MINAS GERAIS, BRAZIL [1]

(with 118 figs.)

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The South American dinosaur fauna has become progressively better known, due to successive new fossil findings during the last two decades. Among those findings, the sauropods (huge quadruped, herbivorous dinosaurs) of the clade Titanosauridae play a major role, particularly in Argentina (BONAPARTE, 1996) and Brazil (PRICE, 1951, 1961; KELLNER & CAMPOS, 1997), where remains of the appendicular skeleton are the most common material recovered.

In Brazil, the most important strata which have yielded titanosaurid remains belong to the Bauru Group (Bauru Basin, also known as Alto Paraná Basin), of Cretaceous Age. These strata are located mainly in the Brazilian States of São Paulo, Mato Grosso and Minas Gerais (CAMPOS & KELLNER, 1991; KELLNER, 1996; FERNANDES & COIMBRA, 1996).

The most important titanosaurid fossil collection from Brazil was organized by Llewellyn Ivor Price (Fig. 1), who has collected a great amount of bones from sites near the city of Peirópolis (Fig. 2), close to Uberaba (State of Minas Gerais) between the years of 1947 and 1974 (AZEVEDO & KELLNER, 1998). All material belongs to the Museu de Ciências da Terra - MCT (Earth Sciences Museum) of the Departamento Nacional de Produção Mineral (National Department for Mineral Production) of Rio de Janeiro – DNPM/RJ. This dinosaur collection still remains virtually unknown to Science, except for some preliminary descriptions (POWELL, 1987a; CAMPOS & KELLNER, 1999).

[1] Received on
[2] Programa de Pós-graduação em Zoologia, MN/UFRJ

To the present date, only two species of titanosaurids were formally described in Brazil: *Antarctosaurus brasiliensis* Arid & Vizotto, 1971 and *Gondwanatitan faustoi* Kellner & Azevedo, 1999. Some bone fragments found in the State of São Paulo (Guararapes) were identified just to subfamily level (LEONARDI & DUSZCZAK, 1977). The DNPM/RJ collection, however, is composed by a great amount of titanosaurid bones, in excellent state of preservation and already prepared for study (KELLNER, 1998). This material is specially composed of vertebrae of all types and many girdle and appendicular elements. In spite of the lack of cranial material, the remaining material has great importance for morphological, systematic and phylogenetic studies of sauropod dinosaurs. (SALGADO *et al.*, 1997a; WILSON & SERENO, 1998; SANZ *et al.*, 1999).

Cladistic analysis of the Sauropoda resulted in a great number of sauropod synapomorphies - 17, in the analysis of WILSON & SERENO (1998). Considering that the Eusauropoda comprises all sauropods, except *Vulcanodon*, this number increases to more 40 synapomorphies, resulting in a total of 57 characters which may diagnose a member of the Sauropod clade (again, with exception of *Vulcanodon*). From the first 17, only character n° 2 (sacral vertebral number four or more) does not refer to the appendicular skeleton morphology. At the Eusauropoda level, from 40 characters, only 16 refer to the limb bones. Above the Eusauropoda level, limb bones characters never attain the majority of total synapomorphies at each taxonomic level. The same occurs in the Titanosauridae, where from a total of 20 characters, only 7 refer to the appendicular skeleton (SALGADO *et al.*, 1997a). This suggests that limb bones may still have great potential to yield synapomorphies within higher level taxa, especially within the Titanosauridae.

Therefore, the morphological description of the appendicular skeleton will not only increase the existing data on Brazilian titanosaurids, but will allow further comparisons among them and other titanosaurids of the world (especially from Argentina and Africa). The results of the present study may be useful in building phylogenetic and biogeographical hypothesis in the future.

The present work has three main objectives:

1) To catalogue and identify the sauropod material collected by L.I.Price, recording it within the Fossil Vertebrate Collection of the DNPM/RJ. For this task, we have relied on some help given by Diógenes de Almeida Campos, a

paleontologist who has worked with Price in the DNPM/RJ, and who knows the site of origin of many unnumbered bones from Peirópolis.

2) To describe the morphology of the girdle and appendicular skeleton of the Brazilian titanosaurids, using the collections from both DNPM/RJ and MN/UFRJ.

3) To verify, after the morphological analysis of the Brazilian fossil material.

a) If there is any morphological variation within the material;
b) If this variation occurs, if it does indicate faunal diversity among the collecting sites;
c) If the synapomorphies described in the literature are present or not in the Brazilian bones;
d) If there are clear morphological features which may be used to differentiate the Brazilian material from other known described species, specially the Brazilian, Argentinean, North American, European, African and Asiatic ones;
e) If it is possible to detect morphological variation within these characters, for future utilization in building titanosaurid phylogenetic hypothesis.

BRIEF REVIEW OF THE CLASSIFICATION OF THE SAUROPODA

Since Sir Richard Owen created the Order Dinosauria in 1841, based on similarities bore by three extinct reptiles of gigantic dimensions, which had been found in Great Britain (OWEN, 1842), our knowledge about these curious and awesome beasts has been steadily increasing until present days. Dinosaurs have become so well known for the general public and so explored in the media that they have surpassed the frontiers of Paleontology and are now viewed as genuine products of the media and no longer as mere objects of scientific research. Of all pictures depicting a dinosaur, that of a Sauropod – a huge, elephantine quadruped animal, with a long neck carrying a comparatively small head, peacefully eating some plants near a swamp and striking its also long whiplash-tail from one side to the other, might be the most promptly associated by anyone who has just come up with the word "dinosaur".

The sauropod dinosaurs are traditionally classified within the suborder Saurischia ("lizard-hipped dinosaurs"), together with two other subgroups: the Theropoda (carnivorous bipedal dinosaurs) and the Prosauropoda (mid-sized to large herbivorous dinosaurs, facultative quadrupeds, which flourished along the Triassic). The Prosauropoda is grouped together with the Sauropoda in the Sauropodomorpha, and is considered to be the ancestor group which gave raise to the Sauropoda itself (e.g. BENTON, 1990; CARROL, 1988). Recent studies in which cladistics analysis has been used have confirmed the monophyly of the Saurischia, with a dicotomy leading to the Theropoda and the Sauropodomorpha (e.g. GAUTHIER, 1986). The systematic position of the Prosauropoda in relation to the Sauropoda (if it is a monophyletic sister group of the Sauropoda, or a paraphyletic assemblage of successive taxa leading to them) is still matter of dispute.

The sauropod dinosaurs flourished mainly in the Jurassic, when many forms attained great size (surpassing 30 meters in length), probably weighting up to 80 tons. After that, their populations dwindled in the Northern Hemisphere, being progressively substituted by ornithischian dominated herbivorous faunas. Nevertheless, the Sauropoda members survived in the southern paleocontinent Gondwana, where they thrived throughout the Cretaceous, until the great extinction that closed the Mesozoic.

The sauropod dinosaurs are characterized by their obligatory quadrupedal posture, possession of long neck and tail, and comparatively small heads in relation to body size. Skulls rarely fossilized with the skeleton, resulting in loss of important information for the study of sauropod anatomy and relationships. The gap is filled in part by the detailed study of vertebral anatomy. The great size attained by these terrestrial animals, with a consequent increase in weight that the body had to support, demanded an anatomic response of their skeletons, and the axial system underwent several adaptations to enlighten the vertebral elements. So, the sauropods developed a series of excavations (to release weight) and laminations (to bone reinforcement) in their vertebrae, specially the cervicals and dorsals. Each genus has its own set of diagnostic vertebral features, so vertebral anatomy began to play a major role in sauropod identification and classification (McINTOSH, 1990: 345).

Sauropods did not live in swamps as once thought, but inhabited the land. The icnological evidence favors the vision of sauropods as terrestrial animals. It suggests also that sauropods were gregarious animals, living in herds (DODSON, 1990: 403). The

icnological evidence further suggests that, when walking, sauropods did not drag their long tails, but kept them raised above the ground.

The history of the Sauropoda begins with O. C. MARSH (1878). This author coined the name as a suborder of the Saurischia ("lizard-hipped dinosaurs") to accommodate quadruped dinosaurs of gigantic proportions, with herbivorous feeding habits, endowed with long necks and tails, and morphological complex dorsal vertebrae. At first, Marsh included only one family within his Sauropoda - the Atlantosauridae. As new species were discovered latter, he successively created new families – such as Morosauridae, Diplodocidae and Pleurocoelidae – expanding the classification system of the original Sauropoda (MARSH, 1895, 1898, *apud* WILSON & SERENO, 1998: 2). Other authors have also contributed, adding new families to the original scheme of Marsh, both extending and modifying it (McINTOSH, 1990; WILSON & SERENO, 1998: 2).

One of the authors to contribute to the study of Sauropods was LYDEKKER (1877), who completed some studies on the vertebrate fossils of India, describing then *Titanosaurus indicus*, a dinosaur characterized by its unusual procoelic caudal vertebrae. LYDEKKER (1885) continued to study the vertebrates of India, proposing the family Titanosauridae, contributing thus to the expansion of the Sauropod classification of Marsh.

Since then, the Titanosauridae was accepted by most authors (HUENE, 1927, 1929), although some of them (JANENSCH, 1929) positioned it at a lower rank - as the subfamily Titanosaurinae, within the Homalosauropodidae (JANENSCH, 1929). Regardless of the rank occupied by the members of the Titanosauridae, they were always considered to be at equal level with the Diplodocidae, Apatosauridae and Dicraeosauridae (sauropods which had peg-like teeth), opposed to the forms with chisel-like teeth, represented mainly by the Camarasauridae and Brachiosauridae, and by a number of primitive forms collectively lumped together as the Cetiosauridae (all positioned within the Bothrosauropodidae).

ROMER (1956) elaborated a classification scheme where the Titanosauridae comprised all four families (lowered to subfamily level) of the Homalosauropodidae, becoming thus a synonymous of the latter.

The classification scheme proposed by Romer lasted along the sixties and seventies, when new discoveries, particularly in Africa and China, and the increasing accumulating data on Sauropod dinosaurs led the majority of the authors to accept a more stable classification system based in six families: the Vulcanodontidae; the Cetiosauridae, the

Camarasauridae, the Brachiosauridae, the Diplodocidae and the Titanosauridae (BONAPARTE, 1986; NORMAN, 1985; CARROLL, 1988; BENTON, 1990; McINTOSH, 1990; McINTOSH, BREET-SURMAN & FARLOW, 1997).

In this classical classification system, the Vulcanodontidae Cooper, 1984 is represented by a single species – *Vulcanodon caribaensis* Raath, 1972, from the Triassic-Jurassic boundary of Zimbabwe. It is known for an incomplete skeleton, lacking the skull. It is regarded as the most primitive sauropod (McINTOSH, 1990; WILSON & SERENO, 1998).

The Cetiosauridae Lydekker, 1888 is a assemblage of generalized, geographically widespread, Middle to Late Jurassic sauropods, including a great number of genera, such as *Cetiosaurus* (England), *Patagosaurus* (Argentina), *Shunosaurus* (China) and *Haplocanthosaurus* (USA). This family is probably a paraphyletic group, still waiting for a revision.

The Brachiosauridae Riggs, 1904 is best represented by the genus *Brachiosaurus*, from the Upper Jurassic of Africa and the United States of America. There are, however, several other species classified within this family, extending its temporal range from the late Jurassic to the early Cretaceous (McINTOSH, 1990: table 16.1).

The Camarasauridae Cope, 1877 is represented only by the well-known genus *Camarasaurus*, from the Late Jurassic of the United State of America (Morrison Formation). This genus is known from all parts of the skeleton, including the skull. One specimen has been found almost fully articulated, making *Camarasaurus* the best known sauropod of all.

The Diplodocidae Marsh, 1884 is the family with the greatest number of well-known forms, with several skeletons and skulls described. McINTOSH (1990) recognizes three subfamilies within the Diplodocidae: Diplodocinae (represented by the North American genera *Diplodocus*, *Barosaurus*, *Apatosaurus*, and *Amphicoelias*); Dicraeosaurinae (represented by *Dicraeosaurus* in Africa, *Nemegtosaurus* and *Quaesitosaurus* in Mongolia, *Rebbachisaurus* in Morocco and by *Amargasaurus* in Argentina); and Mamenchisaurinae (represented by *Mamenchisaurus* from China)

The Diplodocinae and the Mamenchisaurinae are restricted to the Upper Jurassic; the Dicraeosaurinae has representatives from the Upper Jurassic (*Dicraeosaurus*) and both lower (*Rebbachisaurus*) and Upper Cretaceous (*Nemegtosaurus* and *Quaesitosaurus*).

Finally, the Titanosauridae was a successfully group of sauropods, with probable origin in the Late Jurassic, which survived extinction, flourishing specially along the Late Cretaceous and spreading themselves over a wide geographical range comprising Europe, Africa, Asia, Australia, North and South America. They are characterized, among several features, principally by their unusual procoelic centra of the anterior caudal vertebrae, with well-developed ball-and-socket articulations.

This six-family system is not devoid of occasional debates, and a number of other families have been proposed or accepted by some authors in their own classification systems: the Chubutisauridae (CORRO, 1975); the Dicraeosauridae (BONAPARTE, 1986); the Andesauridae (BONAPARTE, 1996); the Euhelopodidae (CARROLL, 1988; UPCHURCH, 1995); the Nemegtosauridae (UPCHURCH, 1999) are just a few examples.

With the advent of Phylogenetic Systematics (Cladism), researchers began to build up cladograms depicting the phylogenetic relationships of the Dinosauria. The first one dealing with the Sauropoda was that of GAUTHIER (1986) - in fact, a classical work on the Saurischian dinosaurs and the origin of birds. Gauthier's work immediately achieved at least two important goals: first, the realization that the Sauropoda could be separated in a group of successive primitive forms (*Vulcanodon* and *Barapasaurus*) opposed to the most derived forms, represented by four of the classical families; second, the distribution of these families in two sister clades: the "Camarasaurs" (Camarasauridae and Brachiosauridae), and the "Titanosaurs" (Diplodocidae and Titanosauridae) attesting thus the monophyletic nature of each family.

Gauthier's work was a harbinger of future changes in Sauropod phylogenetic theories, which would show most important results along the nineties. Several researchers published important works on Sauropod phylogeny then: UPCHURCH (1995); CALVO & SALGADO (1995); SALGADO, CORIA & CALVO (1997a); WILSON & SERENO (1998); SANZ *et al.* (1999). Each one has come up with its own phylogenetic scheme and classification system, but two of them (SALGADO, CORIA & CALVO, 1997a; WILSON & SERENO, 1998) have both matched in rearranging the relationships of the four main sauropod families, modifying the previous dicotomic scheme of Gauthier (which, by its time, was coincident with the classical classification system).

The two above cited works agreed with Gauthier's analysis by positioning a series of successive primitive taxa (*Vulcanodon*, *Shunosaurus*, *Barapasaurus* and *Omeisaurus*)

until reaching a clade of Late Jurassic and Cretaceous forms, named Neosauropoda (Figs. 3 and 4).

The Neosauropoda, in turn, was split into a Diplodocidae (SALGADO *et al.*, 1997a) or Diplodocoidea (WILSON & SERENO, 1998) clade, opposed to its sister group composed of all remaining derived Sauropods. This sister group is the Camarasauromorpha in the analysis of SALGADO *et al.* (1997a) or the Macronaria of WILSON & SERENO (1998) (which included *Haplocanthosaurus* + the same Camarasauromorpha).

The Camarasauromorpha is split into the Camarasauridae (in SALGADO *et al.* 1997a) or *Camarasaurus* (WILSON & SERENO, 1998) and its sister taxon, the Titanosauriformes.

The Titanosauriformes is then split into the Brachiosauridae (WILSON & SERENO, 1998) or *Brachiosaurus* (SALGADO *et al.* 1997a) and its sister group Somphospondyli (*Euhelopus* + Titanosauria in the analysis of WILSON & SERENO, 1998) or the unnamed taxon I in the analysis of SALGADO *et al.* (1997a) (these authors have not included *Euhelopus* is their analysis).

The classification system of the Sauropoda based in the two above works may be summarized as follows (Figs. 3 and 4):

SAUROPODOMORPHA
- Prosauropoda
- Sauropoda
  - Neosauropoda
    - Diplodocoidea or Diplodocidae
    - Macronaria
      - *Haplocanthosaurus*
      - Camarasauromorpha or *Camarasaurus*
        - Titanosauriformes
          - Brachiosauridae
          - Somphospondyli
            - *Euhelopus*
            - Titanosauria

The analysis of WILSON & SERENO (1998) stops at the Titanosauria, but that one of SALGADO *et al.* (1997a) goes further, trying to clarify Titanosaurian relationships. The work of SANZ *et al.* (1999), also deals with phylogenetic relationships within the Titanosauridae, and both works will be discussed in the next section.

Traditionally, the Sauropoda are recognized by several features, such as: very large body size, relatively small skulls, long necks, long tails, skull with large dorsally placed nares, greatly reduced jugal, usually excluded from the ventral border of the skull, large quadratojugal, relatively small endocranial capacity, highly vaulted palate with large pterygoids, presacral centra lightened by deep pleurocoels and or cancellous bone, neural arches and spines largely reduced to a complex of thin laminae, 12 to 19 cervicals, 8 to 14 dorsals, scapula oriented more nearly horizontal than vertical, ilium with broadly expanded preacetabular process and with pubic peduncle much longer than ischial, limb bones robust and solid, no notch between head and greater trochanter in femur, carpus and tarsus reduced to one or two elements each, in all but perhaps the earliest forms, metacarpals longer than metatarsals, number of phalanges greatly reduced in manus, digit I alone retaining a claw, number of phalanges reduced in digits IV and V of pes (MCINTOSH, 1990: 354).

Recently, the evolution and phylogeny of the Sauropoda have been reviewed by some authors in the light of Phylogenetic Systematics (SALGADO *et al.*, 1997a; WILSON & SERENO, 1998). These works led to the splitting of the Sauropoda in several subgroups, defined by several synapomorphies. A complete list of synapomorphies of the Sauropoda is given in the appendix.

BRIEF REVIEW OF THE CLASSIFICATION OF THE TITANOSAURIDAE

The history of the Titanosauridae begins with LYDEKKER (1877). This author completed some studies on the vertebrate fossils of India, where he had described *Titanosaurus indicus*, a dinosaur characterized by its unusual procoelic caudal vertebrae. Lydekker continued to study the vertebrates of India, and, in 1879, he described another species of *Titanosaurus* – *T. blanfordi* (LYDEKKER, 1879). These discoveries led him to propose the name Titanosauridae to accommodate those dinosaurs with unique morphological features in their caudal vertebrae (LYDEKKER, 1885). Lydekker contributions to the Titanosauridae would expand abroad, during a visit to Argentina,

where he studied and described new dinosaurian material from that country, identifying it also as titanosaurid, thus extending the range from that family from India to South America LYDEKKER, 1893). In his work, Lydekker described a new species of *Titanosaurus* – *T. australis*, based on a large collection of vertebral series and isolated limb bones; as well as a new genus and species, *Argyrosaurus superbus*, based on a huge articulated anterior limb skeleton, including the metacarpals.

DEPERET (1896) identified two caudal vertebrae from Madagascar as a new *Titanosaurus*, and named *it T. madagascariensis*. A scute was found together with those remains, which made Deperet suggest that Titanosaurids could bear body armor.

Hypselosaurus priscus Matheron, 1869 (isolated postcranial remains of at least 10 individuals) and *Macrurosaurus semnus* Seeley, 1869 (caudal vertebrae sequence) are other discoveries of the 19th century which were later identified as Titanosaurid members, proving that members of the family were around along the Cretaceous of Europe.

The beginning of the 20th century was especially profitable in titanosaurid findings.

STERNFELD (1911) studied *Gigantosaurus robustus* Fraas, 1908 - a huge sauropod from the Tendaguru beds (Upper Jurassic of Tanzania), and established a new genus - *Tornieria*, replacing *Gigantosaurus*, which was preoccupied (JACOBS *et al.* 1993)- . *Tornieria* is, thus, the oldest known titanosaurid, although problematic, for some of the original material (especially limb bones) may not have belonged to it (McINTOSH, 1990: 397).

HUENE (1927) examined some material from the late Cretaceous of Colina (São Paulo) and identified a caudal vertebra as belonging to a *Titanosaurus*, possibly *T. australis*, so becoming the first record o the Titanosauridae in Brazil (CAMPOS & KELLNER, 1999: 143).

HUENE (1929) followed the footsteps of Lydekker and went to Argentina, in order to study lots of dinosaurian material collected by Wichmann and collaborators throughout the country. By the end of his task, Huene had produced a huge monograph, where he described and illustrated in detail not only the material previously examined by Lydekker, as well as four new species of titanosaurids: *Titanosaurus robustus*, *Laplatasaurus araukanicus* and the gigantic *Antarctosaurus wichmannianus* and *Antarctosaurus giganteus*.

In the following decade, HUENE (1932) revised the Rumanian species *Titanosaurus dacus*, previously described by NOPCSA (1915) and transferred it to a new

genus, *Magyarosaurus*, describing even two more species: *M. transylvanicus* and *M. hungaricus*.

In that same year STROMER (1932) described another species, *Aegyptosaurus baharijensis*, which he had unearthed during an expedition to the Sahara desert, Egypt. The discovery of *Aegyptosaurus* extended the geographical range of the Titanosauridae to the African continent. Unfortunately, this species was destroyed during World War II.

GILMORE (1922) had reported a new sauropod species from the Upper Cretaceous of New Mexico (USA), based on a left scapula, which he named *Alamosaurus sanjuanensis*. The titanosaurid identity of this species was finally confirmed in 1946, with the discovery of an articulated incomplete skeleton of *Alamosaurus* (GILMORE, 1946). The specimen had a complete articulated forelimb and manus, plus the scapula fused with the coracoid, both sternal plates (which had fossilized in articulated manner), the sacrum (which was left in the field), a series of 30 articulated caudal vertebrae and a pair of ischia. The profusion of articulated material made *Alamosaurus sanjuanensis* the most complete and better known titanosaurid of all. Besides, it showed that the family survived into the Cretaceous of North America, where sauropod remains were abundant only in Jurassic beds.

SWINTON (1947) reported new discoveries of *Titanosaurus indicus*.

In Brazil, L.I. Price unearthed a large amount of titanosaurid bones, between the forties and the seventies (PRICE, 1951; CAMPOS & KELLNER, 1999). The discoveries were made in the State o Minas Gerais, mainly around the city of Uberaba, revealing several quarries, rich in titanosaurid materials, including eggs (PRICE, 1951). Price, who organized a great collection at the Paleontological sector of the Departamento Nacional de Produção Mineral of Rio De Janeiro (DNPM/RJ), passed away before he could study these materials. More details about these findings are given in a latter section of this work.

Although Price has never described the DNPM/RJ material, other titanosaurid findings were reported in Brazil by some authors. In 1971, ARID & VIZOTTO (1971) described a new species of titanosaurid, which they named *Antarctosaurus brasiliensis*, based in scrappy remains found in São José do Rio Preto (São Paulo). LEONARDI & DUSZCZAK (1977) reported some fragmentary remains from Guararapes (São Paulo) which they referred to the Titanosauridae Titanosaurinae. Ten years latter, a more complete titanosaurid skeleton was found in Álvarez Machado (São Paulo) by a crew of the Museu Nacional of Rio de Janeiro (MN/UFRJ) (CUNHA, RÊGO & CAPILLA, 1987).

The pace of titanosaurid discoveries dwindled along the seventies, together with a lost of interest in the study of dinosaurs in general. The scenario changed during the eighties, sparked by the so called "dinosaur renaissance" promoted by BAKKER (1975), OSTROM (1979), and others.

The resurrection of dinosaurian studies in South America began in the eighties with a series of spectacular findings made by Bonaparte and co-workers in Argentina.

POWELL (1979) reported dinosaurian remains from the Upper Cretaceous of the Salta province. Among them, were pieces of a sauropod, which Powell referred to the genus *Laplatasaurus*. This sauropod had been previously referred to *Antarctosaurus* (BONAPARTE & BOSSI, 1967).

BONAPARTE & POWELL (1980) described the remains of a new titanosaurid - *Saltasaurus loricatus* - the most complete one known to date. The material was composed by many bone pieces of all parts of the skeleton, comprising at least 5 individuals. There were also skull fragments. The most striking feature of *Saltasaurus*, however, was the possession of a mosaic of dermal plates, which covered the back of the animal. The finding confirmed the suggestion of Deperet that these sauropods had body armor.

POWELL (1986) finished a revision of the Titanosaurids of South America. The work was presented as a doctoral thesis dissertation, but, unfortunately, it has been not published to date. In his thesis, Powell revised the old genera and species described both by Lydekker and Huene, and described new ones, such as *Aelosaurus*, *Neuquensaurus* (= *Titanosaurus*).

POWELL (1987b) published a description of *Aelosaurus rionegrinus*, a titanosaurid with rather unique caudal vertebrae. He also visited the Brazilian collections at DNPM/RJ and produced the first preliminary description of the Brazilian titanosaurid vertebrae, which had been collected by Price. These vertebrae comprised cervical, dorsal and caudal elements and were grouped in three series, known as the "A", "B" and "C" series.

POWELL (1990) published a preliminary description of *Epachthosaurus sciuttoi*, from Patagonia, and two years latter, he published a detailed work on the anatomy of *Saltasaurus loricatus* (POWELL, 1992).

The studies on the Titanosauridae in Argentina accelerated during the nineties, when a second generation of researchers began to contribute with their own new findings.

CALVO & BONAPARTE (1991) described *Andesaurus delgadoi*, from the Albian-Cenomanian of Neuquén.

SALGADO & CORIA (1993a) reported new materials referred to the genus *Aelosaurus*, from the Allen Formation of the Rio Negro province. In the same year, BONAPARTE & CORIA (1993) described a gigantic titanosaurid from Neuquén – *Argentinosaurus huinculensis*, whose dorsal vertebra attained more than a meter in height.

Still in the same year SALGADO (1993) published a paper in which he challenged the systematic position of *Chubutisaurus insignis* Corro, 1975 (previously referred to the Chubutisauridae and to the Brachiosauridae), allocating it n the Titanosauridae. Together with Coria (SALGADO & CORIA, 1993b), he made the same in relation to the enigmatic *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka, 1977, from the Upper Cretaceous of Mongolia. In the original description of Borsuk-Bialynicka, this sauropod had been considered a member of the Camarasauridae, whilst any titanosaurid affinities were discarded because the anterior caudal vertebrae of *Opisthocoelicaudia* lacked the procoelic condition typical of the Titanosauridae (they are, in fact, opisthocoelic - the opposite condition found in titanosaurids). SALGADO & CORIA (1993b) listed 16 derived characters shared by both *Opisthocoelicaudia* and the Titanosauridae, considering the opisthocoelic caudals as an autapomorphy of the Asiatic species.

BONAPARTE (1996) published a compilation on the Vertebrate Paleontology of South America, resuming the current information about Argentinean sauropods available until that date.

SALGADO (1996) described a new species – *Pellegrinisaurus powelli*, based on a series of 26 incomplete caudal vertebrae.

SALGADO, CORIA & CALVO (1997b) reported a third specimen of *Aelosaurus*, from the Los Alamitos Formation (Rio Negro province).

In the same year, these three authors made a great contribution to the phylogenetic study of the Titanosauridae, publishing a phylogenetic analysis based on the postcranial material (SALGADO, CORIA & CALVO, 1997a) (Fig. 4). Some of their results were just cited in the Sauropod section, and here we will summarize their conclusions above the Titanosauriformes level:

Titanosauriformes

Brachiosaurus brancai

Unnamed taxon I

Chubutisaurus insignis

Titanosauria

Andesaurus delgadoi

Titanosauridae

Epachthosaurus sciuttoi + *Malawisaurus dixeyi*

Unnamed taxon II

Unnamed taxon III

Argentinosaurus huinculensis

Unnamed taxon IV

Opisthocoelicaudia skarzynskii

Titanosaurinae DGM "B" Series.

Unnamed taxon V

Aelosaurus

Unnamed taxon VI

Alamosaurus sanjuanensis

Saltasaurinae

Neuquensaurus australis

Saltasaurus loricatus

The nineties have also been profitable in works on Titanosauridae from other continents of the world:

JACOBS, WINKLER, DOWNS & GOMANI (1993) published a work on new materials of an Early Cretaceous titanosaurid from Malawi (Africa), *Tornieria dixeyi*, transferring it to a new genus, *Malawisaurus*.

LE LOEUFF (1995) reported and briefly described *Ampelosaurus atacis*, a new Titanosauridae from the Upper Cretaceous from France. The detailed description of this species is still under work by Le Loeuff. He has reported a large amount of material, including a tooth, dorsal and caudal vertebrae, girdle and limb bones, and osteoderms.

JAIN & BANDYOPADHYAY (1997) described a new, rather complete (skull lacking), species of *Titanosaurus* from the Late Cretaceous of Central India, which they named *T. colberti*.

WILSON, MARTINEZ & ALCOBER (1999) reported for the first time a distal tail segment of a titanosaur from the Upper Cretaceous of Mendoza (Argentina).

In the same year, KELLNER & AZEVEDO (1999) described and named the second titanosaurid from Brazil: *Gondwanatitan faustoi*. The specimen was the same, which had been reported from Álvares Machado (São Paulo), in 1987.

In this year also came the second contribution to the study of the material collected by Price. CAMPOS & KELLNER (1999) described three titanosaurid pelves housed at the DNPM/RJ, and concluded that the may have belonged to three different species of titanosaurids. They did not coin formal names to any of those species, however.

SANZ *et al.* (1999) described a new species of Titanosauridae from the Upper Cretaceous of Spain: *Lirainosaurus astibiae*. In the same work, they published a cladogram trying to picture the systematic position of *L. astibiae* in relation to other titanosaurids (Fig. 5).

BONAPARTE (1999) publishes an important work on presacral vertebrae of the Sauropodomorpha, including an extensive analysis of the Titanosauridae presacral vertebrae.

SALGADO & AZPILICUETA (2000) reported a new Titanosauridae species from Argentina, which they named *Rocasaurus muniozi,* allocating it in the Saltasaurinae. At present, another new titanosaurid is under study in Argentina (CALVO, 2001, personal communication) and a new Brazilian specimen from the locality of Prata (Minas Gerais) is being prepared by the Museu Nacional (Rio de Janeiro) staff.

It is expected that the study of these new specimens, as well as the contributions given by the present work, will improve our present knowledge on South American titanosaurids, helping to clarify their phylogenetic relationships.

A more complete understanding of the Titanosauridae relationships is hampered by the lack of skulls. The systematic studies made so far are based mainly in vertebral characters of the vertebrae, specially the caudals (SALGADO *et al.*, 1997a)

A traditional diagnosis of the Titanosauridae is as follows: dorsals with irregularly shaped pleurocoels and spines directed strongly backward; transverse processes directed dorsally as well as laterally, very robust in shoulder region; a second dorsosacral, its rib

fused to ilium; caudals strongly procoelous with a prominent ball on distal end of centrum throughout tail; caudal arches on front half of centrum; sternal plates large; preacetabular process of ilium swept outward to become almost horizontal (MCINTOSH, 1990: 394).

Cladistic analysis of the Titanosauridae (SALGADO *et al.*, 1997a) have yielded several synapomorphies, which are listed in the appendix.

HISTORICAL OVERVIEW OF THE FOSSIL MATERIAL

L.I. Price collected the fossil material under study here during the forties and the seventies. Price had made extensive fieldwork at the surroundings of Uberaba, an important city of the State of Minas Gerais. Near Uberaba, there was a smaller city named Peirópolis. From that locality Price unearthed and gathered the most important dinosaurian collection in Brazil, housing it in the Paleontology Sector of Departamento Nacional de Produção Mineral of Rio de Janeiro (DNPM/RJ), the Government institution where Price worked in. He and his collaborators extracted and prepared hundreds of bones from several outcrops around Peirópolis. The material was excellent, both in quality and quantity. Price planed to describe all material in a great monograph about the Brazilian titanosaurids, when he suddenly passed away (CAMPOS & KELLNER, 1999). After Price's unexpected death, the Peirópolis material was abandoned, and it was not even cataloged or included in the fossil vertebrate collection of DNPM/RJ.

Some vertebral sequences received just a preliminary description (POWELL, 1987a). Besides, three almost complete pelves were recently described, and it has been suggested that each one belonged to a different species (CAMPOS & KELLNER, 1999). All other bones, referred mainly to the appendicular skeleton, remained still undescribed.

The material here under study has come from three main fossil sites around Peirópolis: "Site 1", "Rodovia" and "Serra da Galga" (according to Price's terminology, described in CAMPOS & KELLNER, 1999). Unfortunately, after his death, Price's field notes were lost, and together with them, valuable information about these sites.

The best material has been unearthed from "Site 1" (Fig. 6). This is the only site recorded in a field map (CAMPOS & KELLNER, 1999). The site "Serra da Galga" has yielded interesting remains, and the "Rodovia" site has contributed only with a few bones.

GEOLOGICAL SETTING

The Paraná basin is an extensive depositional area (1.600.000 km^2), comprising four South American countries: Brazil, Paraguay, Uruguay and Argentina. In Brazil, the strata of the Paraná basin cover the states of São Paulo, Paraná, Santa Catarina, Rio Grande do Sul, Mato Grosso, Mato Grosso do Sul and Goiás, comprising an area of 1.000.000 km^2.

The dinosaur bones under study herein have come from sedimentary strata located near the cities of Uberaba and mainly Peirópolis (State of Minas Gerais). These strata lie within the area of the Bauru basin (or Alto Paraná basin), a sedimentary unit, which was formerly considered as a sub-basin of the Paraná basin (Fig. 7).

The sediments vary in age from Paleozoic (Devonian to Permian) to Mesozoic (mainly Triassic and Cretaceous).

The Paraná basin is limited and divided by a series of important geologic arches, leading to its subdivision in five sub-basins: a) Alto Paraná; b) Paranaense-Catarinense; c) Uruguaia-Sul-rio-grandense; d) Chaco-Paraná and e) Ocidental (PETRI & FÚLFARO, 1983: 29).

The Alto Paraná sub-basin comprises the Brazilian states of São Paulo, Minas Gerais (where the cities of Uberaba and Peirópolis are located) and Goiás. Recently, the geological aspects of this sub-basin led some authors to consider it a basin itself, naming it Bauru basin (FERNANDES & COIMBRA, 1996).

The Bauru basin is a depression developed in the south-central of the South American Platform by thermo-mechanical subsidence in the Late Cretaceous, following the rupture of the Gondwanic continent and the opening of the Atlantic Ocean.

The Bauru basin extends itself over an area of 370.000 km^2, comprising the Brazilian states of São Paulo, Paraná, Mato Grosso do Sul, Minas Gerais and Goiás. The sedimentary sequence is about 300 m thick.

The Upper Cretaceous sequence is formed by two chronocorrelative groups: Caiuá and Bauru (Fig. 8). Both have a discordant contact with the underneath basaltic deposits known as Serra Geral Formation. They are composed by a continuous sequence of siliciclastic continental rocks with local association of volcanic ones.

The Caiuá group comprises three formations: Santo Anastácio; Rio Paraná and Goio Erê, and bear no importance for the present work.

The Bauru group (origin of the bones herein studied) comprises the Adamantina, Uberaba and Marília Formations. This group comprises fluvial and alluvial fans deposits The fossil content of the Adamantina and Marília Formations hints at a Santonian-Maastrichitian age (FERNANDES & COIMBRA, 1996: 197). The Araçatuba Formation, represented by outcrops located in the State of São Paulo, is recognized as an inferior sequence of the Adamantina Formation, and is considered of Campanian-Maastrichtian age, based on the fossil ostrachods found there (GOBBO-RODRIGUES, PETRI & BERTINI, 1999).

The Adamantina Formation is composed of fine sandstones, with occasional inclusions of carbonatic matrix and efusive alcaline rocks (Taiúva analcimites). Its fossil contents include fishes, reptiles, mollusks, crustaceans and algae. The environment is interpreted as a braided fluvial system with lagoons, and eolic dunes.

The Uberaba Formation is composed of sandstones, siltstones and mudstones, and basal conglomerates with carbonatic matrix. The fossil content is poor (bone fragments), but eggs have been found. The environment is interpreted as a braided fluvial system with lagoons, associated to basal alluvial fans

The Marília Formation is composed by conglomerates and fine-grained sandstone with carbonatic concretions, in a carbonatic matrix. The most frequent sedimentary structures are small to mid-sized cross bedding lamination. The sedimentary package attains 180 m. and the depositional environment is interpreted as being a braided river system with alluvial fans. The Marília Formation is reach in fossils, mainly fishes, amphibians, reptiles (chelonians, crocodilians and dinosaurs), ostrachods and bivalves (FERNANDES & COIMBRA, 1996; BERTINI *et al.*, 1993).

MATERIALS AND METHODS

Fossil material: 72 appendicular and girdle bones from the fossil vertebrate collection of the Museu de Ciências da Terra (MCT) - Departamento Nacional de Produção Mineral do Rio de Janeiro (DNPM/RJ).

The present study was developed in three phases. Each phase corresponds to one of the three objectives exposed in the introductory section.

1.Cataloging and identification of the fossil bones:

This phase was further subdivided in two subphases: a) curatorial activities and b) classification and identification of the material.

a) curatorial activities: systematic numbering of the fossil material, cataloging the bones into the Vertebrate Paleontology Collection of the Departamento Nacional de Produção Mineral of Rio de Janeiro (DNPM/RJ).

b) classification and identification of the material: the fossil bones were classified by site of origin and identified, being then divided into comparable morphological categories, such as scapulae, coracoids, sternal plates, humeri, radii, ulnae, pubes, ischia, femora, tibiae, fibulae and metapodials.

2. Description and Illustration:

This phase was also divided into two subphases: a) morphological description and b) illustration of the bones

a) morphological description: the bones were studied category by category, and their morphology was described. The morphological data was compared with other already described titanosaurid species. The comparisons have been made based in bibliographic consulting and observations made *in loco* when visiting foreign research institutions. These visitations have produced at about 700 photographs, which have been used in the comparative procedures. The following foreign institutions were visited during the elaboration of the present work:

American Museum of Natural History (New York – USA)

Museo de Ciencias Naturales Bernardino Rivadavia (Buenos Aires – Argentina)

Museo de La Plata (La Plata – Buenos Aires – Argentina)

Museo de Geología e Paleontología, Universidad Nacional de Comahue (Neuquén – Argentina)

Museo Provincial de Cipolletti Carlos Ameghino (Cipolletti – Río Negro – Argentina)

Museo Municipal Ernesto Bachmann (Villa El Chocón, Neuquén – Argentina)

The species which have been used for morphological comparisons are listed in the appendix, as well as the abbreviations of the research institutions where they are housed.

b) material illustration: all bones were photographed with a conventional camera (Cannon EOS Elan IIe model). All photos were made in black and white, using either flash light or lateral/oblique illumination (in this case provided by a G.E. 500 watts Photoflood bulb). The lateral illumination was employed to highlight the most important morphological features of the bones.

The photos were scanned by a Minipa scanner, digitalized through Imaging for Windows Millenium. The digital images were then worked out in Paintbrush for Windows Millenium, to compose the plates.

The figures were made in ink, on the base of the photographs. The drawings are just schematic, and their purpose is to show the morphological features of the bone categories described in the text. A list of anatomical abbreviations is given in the appendix.

The figures were then scanned and edited in Adobe Photoshop 6.0.

Along the text, we have mentioned figures and plates of other works and authors. To avoid confusion between those illustrations and the illustrations of the present work, we have left the first in small letter (e.g. fig., pl.) and ours in capital letter (e.g. Fig.).

The scale bar equals 10 centimeters in all figures.

3. Discussion:

In this phase we have analyzed and discussed the results, and tried to answer all questions listed in the third aim.

RESULTS

A total of 71 girdle and limb bones were catalogued into the vertebrate fossil collection of the DNPM/RJ. Each one received an individual number (with the exception of scapulae MCT 1691-R and MCT 1703-R, that were found articulated with their respective coracoids, which have received, therefore, the same number). Humerus MCT 547-R was already catalogued in the collection of DNPM. It was included in the present analysis for its excellent state of preservation, making a total amount of 72 bones studied.

The bones were then separated by site of origin, according to the available information (written on a collection tag, on the bone itself or by personal communication of Diógenes de Almeida Campos – Director of the Paleontological Sector of the DNPM/RJ). They were listed, resulting in their distribution over 6 sites: "Serra da Galga", "Rodovia", Site 1 ("Caieira"), "Peirópolis Surroundings", "Bauru" Group and "Uberaba". The results of this phase are shown in Tables 1 to 6.

Afterwards, the bones were identified by category, so that they could be morphologically compared to each other. They were separated into 11 different categories: scapulae, coracoids, sternal plates, humeri, ulnae, radii, pubes, ischia, femora, tibiae and fibulae. The results of this phase are shown in Table 7. Metapodials were not included in the present study.

The four main sites ("Serra da Galga", "Rodovia", Site 1, and "Peirópolis Surroundings") were analyzed in a separate section – "FOSSIL SITES OF PEIRÓPOLIS", supplemented by Tables 8 to 12.

All bones were studied and morphologically described and illustrated. Tables 13 and 14 present an overview of the titanosaurid appendicular material available for morphological comparisons. The results of the morphological analysis are presented in two sections: "PECTORAL GIRDLE AND ANTERIOR LIMB" and "PELVIC GIRDLE AND POSTERIOR LIMB". These two sections were supplemented by one set of tables and 4 sets of illustrations. The tables include bone information and measurements (Tables 15 to 38). The illustrations include schematic illustrations of girdle and limb musculature (Figs. 9 and 10), schematic dimension drawings (Figs. 11 to 21) morphological line drawings (Figs. 22 to 44) and a set of 74 photographic figures (Figs. 45 to 118).

FOSSIL SITES OF PEIRÓPOLIS

"SERRA DA GALGA"

The bones of this site were unearthed from 1967 to 1973. The excavation work has yielded 18 long bones, among limb and girdle elements. Some vertebrae where also collected, but they are not object of the present work. One metapodial (MCT 1606-R) has been also not included in the present analysis.

All bones had an ink inscription written over them (made by Price), indicating the site of origin and the year of collecting. The exception was tibia MCT 1695-R, whose

provenance site was indicated by Diógenes Campos. The provenance of the "Galga" material is thus reliable.

The "Galga" material is composed of 1 scapula, 2 coracoids, 1 sternal plate, 1 humerus, 2 radii, 3 pubes, 2 ischia, 1 femur, 2 tibiae and 2 fibulae and 1 metapodial. No ulna has been recovered (Table 8).

The two coracoids (MCT 1600/1602-R) are almost the same size, and are among the largest coracoids of the whole material. Unfortunately, both are left coracoids, indicating that the bones from "Galga" do not belong to a single individual.

The left scapula (MCT 1599-R) is too damaged to test whether one of the coracoids articulates with it or not.

The right sternal plate (MCT 1589-R) is large, and well preserved, except for the internal border. The humerus (MCT 1597-R) is robust. These two bones conform in size with the rest of the material.

The two radii found (MCT 1595-R – left and 1598-R - right) differ from each other both in size and morphology, indicating, as the coracoids already did, the presence of more than one individual in the "Galga" material.

Two pubes (MCT 1591/1592-R) and both ischia (MCT 1585/1586-R) form right/left pairs (they are similar to each other in size and morphology). These two pairs seem to articulate one to the other (Fig. 101 – F), so it is possible that both pairs have belonged to the same individual.

The remaining pubis (MCT 1711-R) is the largest within the whole material, indicating the presence of a large individual in this site. It is 30% longer than the other pubes, and displays a different morphology.

The left femur (MCT 1601-R) length has been compared with that of the humerus. The humerus: femur length ratio equals 0.82, a value too high for non-brachiosaurid sauropods (McINTOSH, 1990). Among titanosaurids, this value ranges from 0.71 (*Opisthocoelicaudia*) to 0.74 in *Titanosaurus* (McINTOSH, 1990: 395). For this reason, we considered that the two bones belonged to different animals, further indicating that the "Galga" material is composed by a mixture of individuals.

The two tibiae (MCT 1587-R and 1695-R) are of very different sizes. MCT 1587-R is a small left tibia, while MCT 1695-R is a right tibia 40% larger. The same difference in size is seen between fibulae MCT 1588-R (small) and MCT 1696-R (large). The smaller left tibia (MCT 1587-R) has been compared with the left femur MCT 1601-R. The tibia :

femur ratio equals 0.60. This value seems to low for titanosaurids (0,65 in *Titanosaurus indicus* and 0,69 in *Aegyptosaurus*) and for diplodocines (0,65 to 0,69), being approximate to the non-related diplodocids *Dicraeosaurus* (0,62) and *Apatosaurus* (0,60) (all data from McINTOSH, 1990) . For that reason, we do not believe that these two bones from "Galga" belonged to a single individual.

The small left tibia and fibula bear similar proportions and may have belonged to the same individual. The large fibula (MCT 1696-R) is the largest of all fibulae. Although being a left one, it conforms in size with the large right tibia.

In fact, the largest pubis, tibia and fibula of "Serra da Galga" are also the largest in their respective categories and, therefore, may have belonged to the same individual, but we need more data on titanosaurid proportions to say that with certainty.

"RODOVIA"

As the "Galga" site, this site has yielded both vertebrae and limb bones. Most part of the material had written ink inscriptions indicating the site of provenance and the year of collecting (1967 and 1969). The exceptions are an ulna (MCT 1609-R) and a sternal plate (MCT 1698-R), which had no indication. These pieces were, however, kept together with all other material from the "Rodovia" site, so, through the help of Diógenes Campos, these two bones were also allocated as "Rodovia".

The material of "Rodovia" is meager in relation to the other two sites. It is composed of 2 fibulae, 1 ulna, 1 radius, a fragment of a pubis, two metacarpals and a sternal plate. The metacarpals are not object of the present study (Table 9).

The two fibulae (MCT 1607/1608-R) are both left fibulae, discarding any association of this material with a single individual. The right ulna (MCT 1609-R) and the right radius (MCT 1610-R) are of slightly different sizes, and do not fit well together. The pubis (MCT 1611-R) is only a fragment, and gives not much information. The left sternal plate (MCT 1698-R) is the largest in its category, but it is so tightly encased in a plaster base that it cannot be removed without the risk of turning into pieces. So, the observations on this bone were very limited.

SITE 1 or "CAIEIRA"

This site has yielded the largest amount of material from Peirópolis. Lots of cervical, dorsal, caudal vertebrae, chevron bones, pectoral and pelvic girdle bones, limb bones, metapodials and two virtually complete pelves were unearthed from this site during the years of 1948 to 1959. The richness of the site may be realized by the observation of a field work map elaborated by Price (Fig. 6), where he depicted the digging position of each of the many bones found there (CAMPOS & KELLNER, 1999). The "B" Series cervical and dorsal vertebrae (MCT 1488-R) and the "C" Series caudal vertebra MCT 1490-R (POWELL, 1987a) have come from this site, as well as two pelves – one of the "B" series - and another, isolated – MCT 1536-R (CAMPOS & KELLNER, 1999).

Unfortunately, a great amount of Site 1 bones have been never catalogued, and these have mixed with a lot of other isolated bones, which had also come from Peirópolis surroundings. One of the aims of the present work was to identify the limb bones that belonged to Site 1.

A group of bones could have been identified with certainty, because they were accompanied by information of some sort. This information included either labels or written inscriptions on the own bones. In some cases, the registered year of collecting was the indication to allocate the bone within Site 1 material. We have come up with 15 bones, which we consider to belong to this site with certainty.

The material from Site 1 is composed of 1 scapula, 1 coracoid, 1 sternal plate, 2 humeri, 2 ulnae, 3 radii, 3 ischia, and 2 fibulae (Table 10).

The left scapula (MCT 1652-R) is one of the smallest within the whole material, and belonged to a young individual. The left coracoid (MCT 1653-R) is also as small and must have belonged to a similar young individual. This coracoid articulates with the scapula, although not in a perfect manner (Pl. Small – A, B). This may happen because the articular space between the two bones in the living animal may have been filled with cartilage (scapulae and coracoids of young individuals never fuse). So, we have assumed herein that they were part of the same individual.

The smallest sternal plate (MCT 1713-R) was assigned to "Site 1" on the base of its year of collecting (1958) and because it was stored together with metapodials, ribs and bone fragments also from Site 1. Besides, all material with young proportions comes from this site (Fig. 85).

Two humeri were assigned to Site 1. MCT 1674-R was identified thanks to a photo made by Price (he annotated the provenance behind the photo). This humerus is the smallest of all, attesting further the presence of young individuals in Site 1 (Fig. 85 – D). The other humerus, MCT 1688-R (right) is the largest of all indicating the presence of an older individual.

The two right ulnae of Site1 are of different sizes. The smallest (MCT 1651-R) show young proportions, and may have belonged to the same individual of the scapula or coracoid (Fig. 85 – E).

The other ulna (MCT 1659-R) is a mid-sized ulna, and may have belonged to an individual of intermediate size. These two ulnae have been compared with humerus MCT 1674-R. The comparable ulna:humerus ratio of MCT 1659-R and 1674-R equals 0.77. This value is higher than in *Alamosaurus* (0.65); *Argyrosaurus* (0.69) and *Opisthocoelicaudia* (0.68), but similar to *Aegyptosaurus* (0.75) and *Tornieria* (0.77) (all data from McINTOSH, 1990). The comparable ulna:humerus ratio of MCT 1651-R and MCT 1674-R is 0.68, a value near that of *Argyrosaurus*. We consider this last association plausible, since it is more likely that limb proportions in the Brazilian titanosaurids were similar to other South American species rather than to the African forms (Fig. 71 – C).

Three radii of different sizes and morphologies have been recovered from Site 1. The two left radii (MCT 1648-R and 1649-R) have been associated with the site by their year of collecting. MCT 1648-R cannot be associated with ulna MCT 1659-R (it is longer). MCT 1649-R has similar proportions, but it is a left one, while the ulna is a right one, making impossible any try to articulate them. Therefore, it is not possible to say that they have belonged to the same individual.

The third radius (MCT 1650-R, right) is the smallest of all. It has similar proportions to the small ulna and scapula of this site, and may have belonged to a similar young individual (Pl. Small – F).

Three similar ischia have been found in Site 1. To of them form a pair (MCT 1655-R – right and 1661-R – left). The other (MCT 1654-R) is an isolated bone, distally broken. The presence of these ischia, as well as the two pelves, suggests that some of the pubes listed as "Peirópolis surroundings" may have actually come from Site 1. The morphology of these ischia is different from the ischia found in "Serra da Galga" site.

The two fibulae of Site 1 (MCT 1657-R – left, and 1660-R, right) show the same general morphology, forming a perfect pair. Their proportions in comparison with the rest

of the material correspond to a individual of intermediate size. These fibulae are different from those of the "Rodovia" site and from the large fibula of "Serra da Galga" (MCT 1696-R).

The analysis of Site 1 has so far demonstrated that individuals of at least three different sizes were present among the material. Very small pieces (scapulae, coracoid, sternal plate, humerus, ulna and radius) are indication of the presence of very young individuals in Site 1, and bones of equivalent size have been not found in any of the other two main sites.

PEIRÓPOLIS SURROUNDINGS

This is the largest collection of bones from Peirópolis. It includes several bone categories, with different sizes and morphologies. Many of them are isolated findings, which have been made throughout Peirópolis surroundings. A great many, however, have come from Site 1, but Price passed away before he had cataloged all bones, and now all the information is lost. We have managed to associated some of these bones with Site 1 by indirect ways. Some bones are known to have com from neither of the three main sites. We are confident, however, that all remaining bones have been unearthed near Peirópolis (and not from other part of the State of Minas Gerais or Brazil). The sites "Serra da Galga" and "Rodovia" cannot be excluded as probably sites of origin at all, but any association is unlikely, since the original bones from these sites had written inscriptions on them.

The material of "Peirópolis surroundings" is composed of 7 scapulae (two of them with articulated coracoids), 1 isolated coracoid, 1 sternal plate, 2 humeri, 3 ulnae, 4 radii, 4 pubes, 2 ischia, 4 femora, 2 tibiae and no fibula (Tables 11 and 12).

MCT 1639-R is a small right scapula. It is the same size as the small scapula MCT 1652-R from Site 1, with which it makes a perfect pair. For this reason, and because Site 1 was the only site to have yielded material from young individuals, we have considered that MCT 1639-R has also come from Site 1.

The association of the remaining scapulae with Site 1 is unlikely, since the map of Price does not show a clear silhouette of any.

MCT 1680-R (right) is a mid-sized scapula, and the best preserved of all. This scapula has been compared with left humerus MCT 1674-R. The length of humerus : length of scapula ratio equals 0.92. This is the same value found for *Alamosaurus*

sanjuanensis (GILMORE, 1946: 36-37). This suggests that these two bones could have belonged to animals of the same size (Fig. 85 – C, D).

MCT 1642-R is a larger scapula, but it is too broken and eroded, contrasting with the superb preservation state of Site 1 bones. Therefore, it must have come from other site.

MCT 1691-R and MCT 1703-R (both left) are the only scapulae preserved with their respective coracoids articulated. They are important, for they show distinct morphologies. Scapula MCT 1703-R has a collecting code (DGM 810 LE) that may help to unveil its origins.

MCT 1708-R (right) and 1709-R (left) are the largest scapulae of all. They are not a pair, for MCT 1709-R the largest of the two. They show some unique morphological features. These scapulae have not come from Site 1 for sure, because they would have been indicated by distinct drawings in the map of Price if so.

The isolated right coracoid MCT 1710-R is the largest of all. It is not large enough, however, to have belonged to neither of the largest scapulae. It state of preservation is poor, so we have discarded any association with Site 1.

MCT 1690-R is a left sternal plate which has been associated with Site 1 according to personal information given by Diógenes Campos.

Humerus MCT 1684-R (right) was compared with ulnae MCT 1659-R (from Site 1) and MCT 1678-R. The ulna : humerus ratio is 0.68 in the first case, and 0.85 in the second. This ratio ranges from 0.65 to 0.68 in other titanosaurids (McINTOSH, 1990). This means that an association of the humerus MCT 1684-R with the ulna MCT 1659-R from Site 1 is very plausible (Fig. 71 – B). If this humerus had come from Site 1 for sure, than it would be the best candidate to articulate with the mid-sized ulna found there.

Humerus MCT 1682-R (left) is one of the largest humeri, being at about 20% larger than the former. It has a collecting code (DGM 811 LE) that may help to identify its origins. We cannot discard Site 1 origins, since this humerus is the same size as MCT 1688-R (from Site 1), and forms with it a left/right pair.

There are three ulnae within the "Peirópolis surroundings" collection. We have evidence to support the association of all of them to Site 1.

MCT 1676-R a left mid-sized ulna that forms a perfect pair with MCT 1659-R. They share the same size and morphology (being distinct from other ulnae). For that reason, we assume with a high degree of confidence, that MCT 1676-R has also come from Site 1 and both ulnae have belonged to the same individual.

MCT 1635-R (left) and MCT 1678-R (right) also share the same size and morphology, making a perfect pair. The year of collecting of MCT 1635 is 1959, a year when Price was working on Site 1. For that reason, we have associated both ulnae with that site. These ulnae are the largest of all. If we calculate the ulna:humerus ratio using the right bones (MCT 1678-R and 1688-R respectively), we obtain 0.67. The same ratio for the left bones ulna MCT 1635-R and humerus MCT 1682-R is 0.66. These values are intermediate to the ratio found in *Alamosaurus* (0.65), *Opisthocoelicaudia* (0.68) and *Argyrosaurus* (0.69). We have a high possibility here of having two almost complete anterior limbs which may have belonged to a large-sized individual from Site 1 (Fig. 71 – A).

From all the four radii present in this assemblage, only one (MCT 1673-R) had a label indicating its origin: "Peirópolis, 1 Km North". Although it is a bit imprecise, it clearly shows that this bone has not come from any of the three main sites.

The radii MCT 1637-R (right) and MCT 1638-R (left) are the same size and morphology, making a perfect pair. These two radii show adequate proportions to make pairs with the mid-sized ulnae MCT 1659-R and 1676-R. They even articulate well with them. For that reason, we have associated both radii with the Site 1 material.

The fourth radius (MCT 1636-R – right) is larger than the previous two, but shows a similar morphology. Its proportions are similar to the large ulna MCT 1678-R, but these two bones do not articulate so well. They possible belonged to two different individuals of similar size. Therefore, the association of MCT 1636-R with Site 1 is uncertain.

There are four pubes in this assemblage.

MCT 1641-R (left) and 1675-R (right) share same size and morphology, forming a perfect pair. MCT 1640-R (right) shows a similar size, but has a different morphology. Although the schematic drawings in Price's map show several large long bones, it is impossible to associate any of them with certainty to one of these pubes. But we cannot discard Site 1 as the possible origin of these bones, since two pelves were present there. It is still to be tested if these pubes articulate with these pelves or not.

MCT 1677-R is the second largest pubis within the whole material. The distal apron is broken. The pubic foramen is closed, indicating an adult. This pubis is too large to have belonged to any of the Peirópolis pelves. None of the bones in Price's map may be associated with it, so it must have come from another site. It Shares some morphological features with MCT 1640-R.

From the two ischia to compose this assemblage, only MCT 1679-R (right) is suspected of having Site 1 origins, because it shares the same size and morphological features with MCT 1654-R, specially a well-developed process for the *flexor tibialis* muscle. It is possible that they make a pair, but they are too damaged to know for sure. This association – two pelves/two pairs of ischia - is plausible in the light of the existing evidence.

There are four femora in this assemblage, and they are all larger than femur MCT 1601-R from "Galga". They are all of different sizes, so none of them can be paired with another.

MCT 1692-R (right) is a robust bone, whose overall shape differentiates if from all other femora, which are slender. MCT 1694-R (left) is too damaged. MCT 1693-R (right) and MCT 1712-R (left) are larger. There is some possibility that these two femora have been unearthed from a different site near Uberaba, so we have assigned them to Peirópolis with doubts. Although both are larger than MCT 1692-R, none of them shows the robust constitution of that bone, being rather slender. They both surpass a meter in length. The largest - MCT 1712-R is about 13% larger than MCT 1693-R.

Right femur MCT 1693-R was compared to right humerus MCT 1688-R. The humerus : femur ratio equals 0,74. This is similar to the 0,72 (*Opisthocoelicaudia*) and 0,74 (*Titanosaurus indicus*) of other titanosaurids (McINTOSH, 1990). Although we cannot claim that they have belonged to the same individual, the association of the two bones on the basis of their proportions is possible. If they really have belonged to one single individual, then we could associate femur MCT 1693-R to Site 1.

There are two tibiae within this material.

MCT 1681-R is a small right tibia, similar in size and shape to MCT 1587-R from "Galga". Since the bones may be paired, it is possible to associate MCT 1681-R to "Galga" deposits. It is the only case in which we have associated a bone to a site other than Site 1.

MCT 1683-R is a large right tibia. We were not able to associate it to any particular site. Calculation of the tibia : femur ratio using the femora two largest femora (MCT 1693-R and 1712-R) result in values of 0,72 and 0,63, respectively. These are higher and lower than the ratios found in *Titanosaurus indicus* (0,65) and *Aegyptosaurus* (0,69) (data in McINTOSH, 1990). These bones may have belonged to different, although similar sized, individuals.

DESCRIPTIONS AND COMPARISONS

PECTORAL GIRDLE AND ANTERIOR LIMB

SCAPULA

In dinosaurs the scapula is straplike, usually three times longer than wide. Its proximal end is proportionally expanded to articulate with the coracoid. The scapulocoracoid in some forms has a discernible acromion process for the articulation of the clavicles, when present (PADIAN, 1997:530).

In the Sauropoda, the scapula and coracoid are free in the juvenile but invariably coossified in the adult. The scapula is an elongated, concave medially, plate that fits against the rib cage (McINTOSH, 1990:365). The proximal end is broadly expanded both dorsally and anteriorly. The acromion divides the expanded portion of the scapula into a large anterior fossa, and a smaller one. The anterior fossa houses the muscle *deltoides scapularis* (McINTOSH, 1990:365). The area of the glenoid cavity is greatly thickened. The shaft is mediolaterally thin. The distal end is variably expanded, being more splayed in brachiosaurids, camarasaurids, and some cetiosaurids (McINTOSH, 1990:365). The distal end is rugose for the attachment of a cartilaginous suprascapula, which is occasionally fossilized (McINTOSH, 1990:365).

The scapula is the area of insertion of several limb muscles (BORSUK-BIALYNICKA, 1977: fig. 6). The most important are: the *serratus* (ser) – a muscle which inserts into the lower margin of the scapular blade. Opposed to it is the *levator scapulae* (lev sc), a muscle which inserts into the distal upper margin of the scapular blade. Over the lateral surface of the scapula, on its expanded proximal end, the *scapulohumeralis anterior* (scha) splays itself over that concave area. The scapula bears a zone for the insertions of a important inferior limb muscle: the *triceps* (tri) . This muscle inserts into the lower anterior tip of the scapula (Fig. 9).

The proximal end of the scapula is variably developed among the different Sauropod families. It is less expanded in *Vulcanodon* than in other primitive "cetiosaurids" sauropods, (eg. *Barapasaurus* and *Cetiosaurus*) whose scapulae look similar. In "cetiosaurids", the proximal end is less expanded than in later forms, and the shaft relatively broad (McINTOSH, 1990:376). The distal end is variably developed. It goes from little (eg. *Shunosaurus*) and moderately expanded (eg. *Barapasaurus, Cetiosaurus,*

Omeisaurus) to widely splayed (*Haplocanthosaurus*) (McINTOSH, 1990). In *Omeisaurus*, the proximal plate of the scapula is more developed than in many cetiosaurids, but still not achieving the same development of later forms (McINTOSH, 1990:380).

In the Brachiosauridae (represented by the well-known *Brachiosaurus*) the scapula is greatly expanded both proximally and particularly distally, where the end is widely splayed (McINTOSH, 1990:383).

In the Camarasauridae (represented by *Camarasaurus*) both the proximal plate and distal end of the scapula are broadly expanded, as in the Brachiosauridae. The angle between the ridge separating the two muscular fossae on the lateral face and the axis of the shaft of the bone is about 66° (McINTOSH, 1990: 385). A large scapulocoracoid attributed to *Euhelopus* shows that the scapula has a well-developed proximal plate and long, relatively slender shaft, which expands regularly toward the distal end, but the expansion, is considerably less than in *Camarasaurus* and *Brachiosaurus*. The coracoid is relatively small, and its border with the scapula exhibits a marked jog upward just above the coracoid foramen (McINTOSH, 1990, 387).

The scapula among the Diplodocidae is represented by several genera; distributed in two subfamilies (the pectoral girdle is unknown in the Mamenchisaurinae). Within the Diplodocinae (represented by *Diplodocus*, *Barosaurus* and *Apatosaurus*), the scapulae have large proximal plates. The distal end is variably expanded, being more so in *Diplodocus*, intermediate in *Barosaurus*, and less in *Apatosaurus* (McINTOSH, 1990). The angle between the ridge on the proximal plate and the shaft is acute in *Diplodocus*, less so in *Barosaurus*, and broad in *Apatosaurus* (McINTOSH, 1990). In the Dicraeosaurinae (represented by *Dicraeosaurus* and *Rebbachisaurus*) the distal end of the scapula is only moderately expanded, the angle between shaft and ridge fairly acute, and a small jog occurred on the scapulocoracoid border above the foramen. In *Rebbachisaurus garasbae*, the blade of the scapula is broad, and the distal end uniquely expands into a broad racket shape (McINTOSH, 1990:394). Equally expanded are the scapulae of *Rebbachisaurus tessonei* and *Rayososaurus*, from Argentina.

In the Titanosauridae (represented by *Saltasaurus*, *Alamosaurus* and *Antarctosaurus*), the scapula has a very stout blade and is little expanded both proximally or distally. It has a long glenoid margin, so that the large quadrangular coracoid articulates farther forward than in most sauropods (McINTOSH, 1990: 395). In *Alamosaurus*, the angle between shaft and ridge on the proximal plate is large. The otherwise straight scapulocoracoid margin is

broken in the middle by a prominent upward deflection. The forward rim of the coracoid projects beyond the scapula (McINTOSH, 1990: 396). The scapula of *Antarctosaurus wichmannianus* has large angle between axis of shaft and muscle ridge, and a coracoid articulation with a short but sharp central deflection (McINTOSH, 1990: 397).

General observations:

There are nine scapulae within the Peirópolis material (Tables 15 and 16, Fig. 11). They show different sizes, representing an assemblage of several individuals, possibly of different ages. The majority of them, unfortunately, have uncertain provenance, so they are almost in totality scored as from "Peirópolis surroundings". The site of provenance is undoubtedly known for only two of them.

MCT 1599-R (left) came from the "Galga" site. It is a large scapula, but lacks the distal end of the blade.

The other scapula of known origin is MCT 1652-R (left). It came from "Site 1", and is the one of the smallest scapulae. It must have belonged to a young individual. This scapula is the same size as the other smallest right scapula of the material (MCT 1639-R). In fact, they are so alike, that they could make a perfect pair. For that reason, we considered its site of origin to be also "Site 1". These two small scapulae are very well preserved, only the distal margin of their scapular blades show some erosion.

All the scapulae commented below have been scored as "Peirópolis surroundings."

MCT 1642-R is a median sized scapula, very damaged. The distal end of the scapular blade is broken, and the scapular plate is almost completely destroyed. Nevertheless it was included in this study because it shows important features, which will be discussed later.

MCT 1680-R is intermediate in size between the smallest scapulae and those two previously described. Its preservational state is excellent, and it is the only scapula in which the distal margin of the scapular blade is complete.

MCT 1691-R is almost the same size as MCT 1680, but differs a little in general proportions. It is well preserved, except for the damaged acromial surface, and articulated with its respective coracoid.

MCT 1703-R is a large scapula, whose blade is distally broken. As the previous one, this scapula was preserved with its respective coracoid articulated to it.

The last two scapulae to be considered are MCT 1708-R and MCT 1709-R. They are the largest of all. The first one has a damaged acromion and a blade distally broken. The other is the largest of the two, and its coracoidal articular area is very damaged. Both of them display an overall heavy construction and their blades bear interesting features, which will be discussed below.

Morphology:

The scapula longest axis displays an oblique, nearly horizontal orientation in relation to the rest of the trunk, as shown by full skeletal reconstruction of some sauropods, which have been found articulated in the field (GILMORE, 1925: pl. 10; BORSUK-BIALYNICKA, 1977: fig. 19). For the sake of clarity, however, we will standardize the following descriptions considering the scapula as a fully horizontal, paralleled to the ground oriented bone, so that the proximal view envisages all the articular area for the coracoid and the glenoid surface; the superior of upper margin comprises the acromial border plus the upper margin of the blade; the inferior or lower margin extends from the lower tip of the glenoid to the distal lower corner of the blade; and the distal view envisages only the end of the scapular blade.

The scapulae from Peirópolis bear the typical morphology of the sauropod scapula. The bone has a long, medio-laterally flattened shaft. It is not straight, but curved, the medial side being concave and the lateral one convex. This curvature better accommodated the scapular blades over the rib cage.

The bone may be divided in two parts (Fig. 22). The proximal part is the scapular plate (sc pl), the most deeply expanded portion of the scapula, which assumes a rather oval outline. The other distal part is the scapular blade (sc bl), a long and thin backward-projected lamina, which follows the long axis of the whole bone.

In lateral view, the plate is dorsoventrally expanded. The expansion is asymmetrical, since the upper portion is larger than the lower portion. The upper portion arises abruptly from the dorsal margin of the blade being very thick in this region. This thickening marks the presence of a vertical, cylindrical spine – the acromion (acr). In other sauropod scapulae, the acromion delimitates anterior and posterior concavities, which house muscles of the pectoral girdle. In all the scapulae from Peirópolis (and in all

titanosaurids but *Antarctosaurus*) however, the posterior concavity is absent, since the acromion arises immediately in front of the base of the blade.

The acromion spine extends itself over the upper half of the plate. It is set at a right angle to the long axis of the blade. Its superior border tapers gradually forwards, so that the upper border of the plate becomes progressively thin.

In proximal view, this thin border descends, following the coracoidal articular margin (cor art mg). Than, the anterior border thickens gradually along the upper third of the plate. In the beginning of the second third, the plate suffers a great medio-lateral expansion, which assumes an irregularly oval profile. This oval area is very convex laterally, sinuous, and a bit concave medially. It may be decomposed into an upper and a lower subtriangular area, united in the middle by their respective bases. The upper subtriangular area corresponds to the coracoidal articular surface (cor art sf). The lower subtriangular area points out downwards, and corresponds to the glenoid surface (Fig. 23 - gl). The coracoidal articular surface is all marked by rugosities. The glenoid surface is less rugose, and covered by several deep grooves.

The proximal margin of the plate, in lateral view, shows an oblique line, which descends from the uppermost point of the plate (over the acromion), to its middle. There, this line suddenly curves downwards, assuming a vertical orientation, more or less perpendicular to the longest axis of the blade. The line finishes in the lower corner of the glenoid, forming a pointed tip. The oblique line is not continuous, but shows an indentation (Fig. 24 – A - ind) for the articulation with the coracoid. This indentation is slightly marked in the smaller scapulae (MCT 1639-R, MCT 1652-R and MCT 1680-R), but is strongly evident in the larger ones.

The inferior border of the plate displays an elevation, probably for muscle attachment, which is placed just in front of the beginning of the scapular blade. If this scar proves to be the insertion area for the muscle ***serratus*** (BORSUK-BIALYNICKA, 1977, fig. 10) than it is too forwardly displaced (Fig. 22 – A – m.ser).

The blade of the scapula is a long, backward projection, which stems from the rear portion of the plate. It is more or less rectangular in lateral view. The lower margin is more or less straight, while the upper one is a slightly concave curve. The width of the blade is not uniform along all its length, but shows a slight constriction approximately in the anterior half. This constriction corresponds to the point where the width of the blade is minimum. From that point on, both upper and lower margins diverge gradually and the

blade tends to get wider until reaching the distal end, which is a little expanded. The distal end is medio-laterally flattened, and very rugose.

The anterior third of the medial face of the blade is concave. This concavity extends itself until the point where the blade has its minimum width. Than, from that point on towards the distal end, the medial surface assumes a planar aspect.

The lateral surface is marked by a strong convex surface (cvx sf), which extends itself almost over the entire length of the blade, disappearing near the distal third, where, like the medial surface, it assumes a planar aspect (Fig. 22 – A).

The upper margin is thin and laminar, the lower one is thicker. The blade has a "U" shaped outline in cross section in all scapulae but in the largest ones (MCT 1708 and 1709). In these, whose lower margins attain a considerably thickening, the blade is "L" shaped and deeply concave medially (Fig. 52 – E).

The blade is a little twisted, so that, in superior view, the inferior distal corner is slightly outwardly directed, while the upper margin stays straight. There are only two scapulae (MCT 1691 and MCT 1703) which have been found with their respective coracoids (Fig. 23). These were never coossified to the scapular plate, which suggests that none of the specimens under study had already attained full adult size. The coracoids are described in a separated section. The mode of articulation of the coracoids with their scapular plates is discussed below, along with the individual description of each bone.

The majority of the scapulae from Peirópolis bear a medial prominence (med prm) placed on the internal side of the blade, near its upper margin. The presence or absence of this prominence is the base for distinguishing two morphotypes (Fig. 23).

Two morphotypes were recognized for the scapula:

Morphotype 1

Material: MCT 1642-R and MCT 1703-R.

Description: in morphotype 1, the upper medial border of the scapula is continuous and flat, lacking any prominence.

MCT 1642-R (left) (Fig. 45 – C): this is a mid-sized scapula, almost the same size of MCT 1599. The site of origin is unknown, so it was scored as "Peirópolis surroundings". This scapula is badly preserved. The distal blade is broken and lost, and almost all the plate is destroyed by erosion. Nevertheless, the preserved portion is in good state enough to record the absence of a medial prominence among the Peirópolis material. The area where this prominence should be is smooth, although cracked. The medial surface is flat, instead of being concave as in all other scapulae.

MCT 1703-R (left) (Fig. 23 – A; Fig. 51): this is a large scapula, in which the coracoid has been also preserved articulated. The site of origin is scored as "Peirópolis surroundings". This scapula is very well preserved, particularly in the articular coracoidal and glenoidal surfaces. It does not bear any medial prominence on its scapular blade. The absence of the character is however doubtful, since this scapula has been broken in two parts exactly in that point were the prominence should be. The area became so a little bit cracked to know for sure. Nevertheless, it was classified within the morphotype 1 category. The anterior articular coracoidal margin bears the indentation yet described. The scapular glenoid is strongly beveled medially and almost two times longer than the coracoidal glenoid surface. The glenoid cavity forms a 90° angle (as in MCT 1691-R). The blade of MCT 1703-R, however, is not short as in MCT 1691-R, displaying normal proportions. The coracoidal articular surface, as well as the scapular glenoid area show the best state of preservation of all scapulae. The coracoidal articular surface is rugose, ending in a horizontal ridge which articulates with the coracoid and delimitates the beginning of the glenoid area, which is very expanded. In anterior view, the glenoid displays a large heart-shaped facet, its vertical length comprises at about 50% of the total height of the scapula. The medial half is oval and bears a strongly convex medial border, marked by several short grooves. The lateral half margin is more of less straight. Its surface is criss-crossed by grooves. There is a deep groove, which runs obliquely from the upper lateral margin of the glenoid to its medial margin below. This groove is also present in MCT 1680-R, but absent in the smallest scapulae (MCT 1639-R and MCT 1652-R), MCT 1599-R and MCT 1691-R. The other scapulae are not so well preserved in this area to tell for sure.

The articulated coracoid is not fused to the plate. As in MCT 1691-R, its posterior border bears a jog, which articulates to the indentation of the anterior border of the scapular plate. MCT 1703-R differs from MCT 1691-R, however, because the upper margin of the coracoid projects itself a little beyond the upper margin of the scapular plate.

Morphotype 2

Material: MCT 1599-R, MCT 1639-R, MCT 1652-R, MCT 1680-R, MCT 1691-R, MCT 1708-R and MCT 1709-R.

Description: in morphotype 2, the medial prominence is present on the inner face of the scapular blade, near its upper margin. The prominence shows some degree of morphological variation, ranging in shape from a longitudinal or oblique ridge to a rounded elevation.

This prominence is different from that found in the Saltasaurinae (SALGADO *et al.* 1997a), for this prominence arises directly as a projection from the upper margin of the scapular blade, turning medially, being even a little pointed (personal observation on an undescribed Saltasaurinae of Argentina). The presence of this feature in the Brazilian material approaches it to *Aelosaurus*, *Alamosaurus sanjuanensis* and *Lirainosaurus astibiae*.

MCT 1599-R (left) (Fig. 45 – A, B): this is the only scapula, which comes from the "Galga" site. This is a median sized scapula, which is too damaged. The distal blade is broken and the articular area of the plate is eroded. The medial prominence is however present, which allows its allocation into the morphotype 2 scapulae. The medial prominence takes form of a strong ridge, obliquely oriented. The muscle scar of the lower border of the plate (muscle *serratus*?) in this bone is particularly well developed, rugose and prominent.

MCT 1639-R (right) (Fig. 46 – A, B; Fig. 47 - B, D) and MCT 1652-R (left) (Fig. 46 – C; Fig. 47 – A, C): these two bones are described together due to their great likelihood. These scapulae are the smallest within the studied material, and both display the normal general morphology of the Peirópolis scapulae. Their blades bear the medial prominence near the upper margin, and it takes form of a longitudinal ridge, parallel to the upper border of the blade. The two scapulae are morphologically very alike, and they share the same proportions, forming a perfect pair. For that reason, we think that they may have belonged to the same individual. The modest size suggests that it was a juvenile.

MCT 1652-R came from Site 1 deposits, and since MCT 1639-R is so similar to it, we have scored its site of origin as Site 1 also. These two scapulae are more curved than others in superior view. The glenoids are beveled medially. The small left coracoid MCT

1653-R seems to articulate with this small scapula. The contact between the surfaces of contact are not at all perfect, and the coracoid is too much displaced medially. It is possible, however, that the space between scapula and coracoid has been filled in life with a patch of cartilage, since it is normal in young individuals to have loosely attached bones.

MCT 1680-R (right) (Fig. 22; Fig. 48): this scapula is one of the best preserved scapulae, and the only one in which the distal end of the blade is fully preserved, without any sign of erosion. This scapula is a little larger than the two previous ones, but bears minute differences in its morphology. The plate is not as high in relation to the total length as the smallest scapulae (the total height:total length ratio of MCT 1680-R is 0.48, against 0.53 in MCT 1639-R). This gives the impression that the bone has a longer scapular blade than others. The medial ridge is also present. It is strongly marked and displays an obliquely orientation, so that its anterior extremity is downwardly curved. The distal end of the blade is symmetrically expanded and its margins are slightly curved. The glenoid is beveled medially and is slightly concave. It bears a strongly marked glenoidal groove (gl gr), also present in MCT 1703-R (Fig. 22 – C).

MCT 1691-R (left) (Fig. 23 – B; Fig. 24 – A; Fig. 49; Fig. 50): this scapula is one of the two scapulae in which the respective coracoid has been preserved articulated to it. It is a medium-sized scapula from "Peirópolis surroundings". It is very well preserved, and shows some features of its own. The scapula belongs in the morphotype 2 category, for it also displays a well-developed medial prominence on its blade. This prominence, however, takes not the form of a longitudinal ridge, being otherwise more rounded. In lateral view, the anterior margin of the plate bears a conspicuous indentation for accommodation of the coracoid. This indentation makes the anterior outline of this margin to turn from oblique to vertical. This trait is also present in all other large scapulae from Peirópolis, suggesting it may be ontological. The scapular glenoid is strongly beveled medially and almost two times longer than the coracoidal glenoid surface, to which it makes a 90° angle. The scapular blade of this bone is a little shorter than in all other scapulae. Its length of blade : total length ratio is 0.57 against 0.63 (MCT 1652); 0.66 (MCT 1680-R), 0.65 (MCT 1703-R) and 0.68 (MCT 1709-R), for instance.

The articulated coracoid is not fused to the plate. Its posterior border bears a jog, which articulates to the indentation of the anterior border of the scapular plate. The upper margins of both scapula and coracoid are set at the same plane in relation one to the other.

MCT 1708-R (right) (Fig. 52) and MCT 1709-R (left) (Fig. 24 – B; Fig. 53): these scapulae are discussed here together, because both of them share unique characters.

These scapulae are the largest of all scapulae among the Peirópolis material (MCT 1709-R, the largest, is almost a meter long). The distal end of the scapular blade of MCT 1708-R is broken, and the acromion spine of MCT 1709-R is eroded. The surfaces of both glenoids are a little eroded, so that they not display clearly the pattern of rugosities and groves which are normally present there.

The most impressive trait of these scapulae is their heavy construction, although expected in animals of great size. The acromion lengths are reduced in relation to the minimum width of the blade (they make 73% in MCT 1708-R and 108% in MCT 1709-R – see Table 17), which is against the character proposed by WILSON & SERENO (1998, character n° 72). Nevertheless, these authors have pointed out that some titanosaurids (such as *Opisthocoelicaudia* and *Saltasaurus*) have reduced the length and relative size of the acromion (WILSON & SERENO, 1999: 46).

In lateral view, the anterior border of both plates bears an indentation. This indentation is better marked in MCT 1708-R. The glenoid is large, strongly beveled medially. Its lower tip is not pointed, but well developed and blunt.

The blades are also heavily built. The ventral margin displays considerably thickening, so that the blade is "L" shaped in cross section. The medial prominence of the scapular blade is present in both scapulae. In MCT 1708-R it is ridge-like and well developed, (although comparatively not so much as in MCT 1599-R). Surprisingly, the medial prominence of MCT 1709-R – the largest of all – is not well developed, taking the aspect of a more of less rounded, low elevation.

The most interesting feature of these scapulae concerns the upper margins of their blades. In all previously studied scapulae, in which the scapular blade is completely preserved, both upper and lower blade margins are straight lines, which diverge gradually from each other in distal direction. In these large scapulae, however, the upper margin of the blades arises abruptly halfway from the distal end, forming an upper expansion (Fig. 24 - B). This expansion is delimited by two elevations (probably for attachment of muscle *levator scapulae*?). The second elevation is placed at about the beginning of the distal quarter of the blade. The portion of the upper margin placed within the two elevations is more of less horizontally oriented, parallel to the lower scapular margin. From that second elevation on, the upper scapular blade descends gradually before reaching the distal border.

Comparisons within morphotypes:

The division of the scapulae from Peirópolis in two morphotypes was based solely in the presence or absence of a medial prominence on the inner surface of the scapular blade. Nevertheless, the morphological analysis attested some morphological variations within morphotype 2 scapulae that may be related to size. Such variations are, for instance, the presence of an upper expansion on the blades of the largest scapulae (MCT 1708-R and MCT 1709-R), their typical "L" shaped cross-section, and the straightening of the acromial length, together with a stronger indentation on the coracoidal articular surface (particularly in MCT 1708-R). We have considered such traits as normal intraspecif variation occurring in the population, but we cannot dismiss the possibility that, with new discoveries in the future, morphotype 2 may be further subdivided in more than one morphotype.

Comparisons with other taxa:

The Peirópolis scapulae have been compared with the following taxa: *Aelosaurus rionegrinus*; *Alamosaurus sanjuanensis*; *Antarctosaurus wichmannianus*; *Argyrosaurus superbus*; *Gondwanatitan faustoi*; *Laplatasaurus araukanicus* (=*Titanosaurus araukanicus*); *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Saltasaurus loricatus*; *Titanosaurus australis* (=*Neuquensaurus australis*) and *Titanosaurus colberti*.

The scapulae of *Antarctosaurus wichmannianus* differs clearly from all the Peirópolis scapulae by possessing a second concavity behind the acromial spine, which is, for its turn, very tall and thin (HUENE, 1929: Iam. 31, fig.1). The scapular blade resembles, however, that of MCT 1709-R, for both of them bear an expanded portion, placed well before the distal end. The plate is also alike in having a slight indentation on the anterior border. Such indentation has been previously noted as a coracoid articulation with a short but sharp central deflection (McINTOSH, 1990: 397).

The holotype of *Argyrosaurus superbus* has no scapula for comparison. The comparisons made herein are based in the additional specimen PVL 4628, referred by POWELL (1986) to the genus but with doubts to the same species (BONAPARTE, 1996: 109). The scapula of *Argyrosaurus* shows a different angle between the longest axis of the blade and that of the acromial-glenoid expansion (BONAPARTE, 1996: 109). This angle is

not present in any of the Peirópolis scapulae, which all show a 90° orientation of the acromial spine in relation to the long axis of the blade. By the drawings available (BONAPARTE, 1996, fig. 43a) one may notice that the scapula of *Argyrosaurus* resembles the scapulae from Peirópolis, mainly the largest ones (MCT 1709-R and MCT 1709-R), in the shape of the scapular plate. It bears some differences in the blade, however. The blade bears an enlargement on its upper margin, before reaching its end, and the lower distal corner is two much expanded, as in *Alamosaurus*. The plate bears a slight indentation on its anterior border, just like the scapulae from Peirópolis.

Based on the right scapula of the hypodigm (PVL 4017-106), the scapula of *Saltasaurus loricatus* differs from the Peirópolis scapulae by bearing an antero-superior border on the blade (POWELL, 1992: fig. 2), which is not present in the Brazilian material. The blade itself is also wider. The medial prominence of the scapular blade is well developed. The anterior border of the plate bears no indentation.

The scapula of *Titanosaurus australis* differs from the Peirópolis scapulae by the shape of its blade, which is more dorsally expanded and also short (HUENE, 1929: lam. 9, fig. 3). Using the measurements given for left scapula MLP/CS 1096 of the hypodigm (HUENE, 1929: 36) the calculated length of blade : total length ratio is 0.57 (the same of scapula MCT 1651-R from Peirópolis). This suggests that a shorter scapular blade may be a character present in adult forms (since the fused scapulocoracoid of *T. australis* indicates that it was a mature individual) and not only a stage of ontological development.

The anterior border of the plate, which articulates with the fused coracoid bears no indentation. The inferior border, which is expanded to receive the *triceps* head, is more developed than in the Brazilian material.

The scapula of *Titanosaurus australis* bears a medial projection on the anterior border as in *Saltasaurus* (BONAPARTE, 1996: 106). The projection is not well figured in HUENE (1929: lam. 9, fig. 3), but, if it has a typical Saltasaurinae shape, than it is different from the projections bore by the Brazilian specimens.

The left scapula of the paratype of *Lirainosaurus astibiae* (MCNA 7459) bears also a medial prominence on the inner face of the scapular blade (SANZ *et al.* 1999: pl.4, c). This prominence seems to be of the same shape as those found in the Peirópolis material. The scapula of the Spanish species is unique, however, in possessing a second longer medial ridge running on the ventral margin of the scapular blade (SANZ *et al.* 1999: 242), a trait absent in any of the Brazilian scapulae.

The scapulae of *Opisthocoelicaudia skarzinskii* (holotype ZPAL MgD-I/48) are very different from any of the Peirópolis scapulae. The acromion is projected a little backwards, and is not so strong developed as in the Brazilian material. The blade is long and strongly curved in relation to the plate (BORSUK-BIALYNICKA, 1977: fig. 6b). The medial prominence is absent. There is a muscle scar on the lateral surface of the blade (BORSUK-BIALYNICKA, 1977: fig. 6c - *m. scapular deltoid* – dsc) which is absent from the Peirópolis material. The scapula is fused to the coracoid, so it is not possible to evaluate the presence of an indentation on the anterior margin of its plate. As in the Peirópolis material, however, the scapula of *O. skarzynskii* is little expanded distally (BORSUK-BIALYNICKA, 1977: 8).

The left scapula of *Titanosaurus colberti* (holotype, ISIR-335/57) is easily distinguished from any of the Peirópolis scapulae for it has a very wide blade (whose breadth makes about 50% of its total length). The distal upper corner of the blade is also abruptly expanded, while the lower corner is squared (JAIN & BANDYOPADHYAY, 1997: fig. 18). This differentiates it from the Brazilian specimens, whose distal blades are slightly expanded upwards. Like in Brazilian morphotype 1 scapulae, however, the medial prominence is absent in *T. colberti* (JAIN & BANDYOPADHYAY, 1997: fig. 18b).

Comparisons with the Brazilian species *Gondwanatitan faustoi* are hindered by the bad preservation of the holotype (KELLNER & AZEVEDO, 1999: fig.17). The only available fragment is part of a left scapular blade, which is unfortunately too damaged to allow good comparisons. The part of the scapula where the medial prominence should be is broken and lost (KELLNER & AZEVEDO, 1999: 131) so this important character cannot be evaluated in this taxon. Therefore, it is not possible to ascribe *G. faustoi* to any morphotype.

Aelosaurus rionegrinus has a broad scapula with distal expanded end, with a prominent and short ridge for muscular attachment near the upper border of the internal face of the scapula, as in *Saltasaurus loricatus* (POWELL, 1987b:148). Although it has never been illustrated, one of us (A.W.A. Kellner) has taken some photos of the holotype (MJG-R1) during a visit to the institution where it is housed (Museum J. Gerholdt, Ingeniero Jacobacci, Argentina). The scapula of *A. rionegrinus* is similar in overall shape to the Brazilian scapulae. It bears a medial prominence, which seems to be morphologically similar to the prominence found in morphotype 2.

The scapula of *Alamosaurus sanjuanensis* (together with that of *Laplatasaurus araukanicus*) is the bone, which shows the closest similarities with the Peirópolis material. There are two specimens available for comparison. The holotype (USNM-10486) is incomplete (GILMORE: 1946, pl.10, fig. 1). The following comparison was based on an additional specimen (USNM-15560), whose complete left scapula has been found articulated with the coracoid (GILMORE, 1946: fig. 6). The blade is long, and the spine is set at right angles to longest axis of scapula (GILMORE, 1946:30). The acromial spine is well developed. The anterior border of the scapular plate shows an indentation for reception of the coracoid. The superior border of the coracoid extends itself beyond the level of the acromial border, just as in MCT 1703-R. The distal end of the scapular blade of *A. sanjuanensis*, however, expands both upwards and downwards, whereas in the Brazilian specimens, the expansion of the distal end is noticed only in the superior corner, the inferior one being almost straight.

Another possible further similarity lays on the presence of a prominence on the medial face of the scapular blade. This character (not figured in GILMORE, 1946) was considered a synapomorphy of a clade uniting *A. sanjuanensis* to the South American forms *Aelosaurus* and the Saltasaurinae (SALGADO *et al.* 1997a). The study *in loco* of the North American species is thus important for further and fruitful comparisons.

In overall shape, the right scapula from the hypodigm of *Laplatasaurus araukanicus* (MLP CS 1031) resembles too much the Peirópolis scapulae. The acromion is well developed, there is no concavity behind the acromial spine, the blade is long, the upper margin of it gradually drifts away from the lower one to form the distal expansion of the blade (HUENE, 1929: lam. 23, fig. 1). On the interior side of the longitudinal anterior border, just before the narrowest portion of the scapula, there is a thickening (about 5 centimeters long), longitudinal oriented, with tapering ends (HUENE, 1929: 57). This character was not figured by Huene, but it seems to be the same medial prominence present in the morphotype 2 scapulae from Peirópolis. The material of *L. araukanicus* must be further analyzed to confirm this similarity.

The scapula of *L. araukanicus* differs from the Brazilian material in one aspect. The anterior border of the plate bears no trace of indentation, being totally straight.

The left scapula attributed by Huene to this species (MLP Av. 1040) differs from the Peirópolis scapulae since the distal end of its blade is more abruptly expanded (HUENE, 1929: lam 23, fig. 2). Huene, unfortunately, did not provide any text description

of this scapula, so it is not possible to make further comparisons without seeing the material.

Characters of the scapula described in previous sauropod phylogenies:

Several characters for the scapula have been described in previous sauropods phylogenetic studies (SALGADO *et al.*, 1997a; WILSON & SERENO, 1998 and SANZ *et al.*, 1999), which are synapomorphical within different levels of their resulting cladograms.

WILSON & SERENO (1998) defined three characters for the scapula: acromion more than 150 percent of the minimum width of the blade (n° 72), scapular glenoid deflected medially (n° 104) and distal blade shape of scapula with rounded expansion on acromial side (n° 109).

The first of these characters is synapomorphic for a lower level taxon, (*Omeisaurus* + Neosauropoda) (WILSON & SERENO, 1998: 45). These authors pointed out that in Prosauropods, the anteroposterior length of the acromion ranges from 100% to 150% of the minimum width of the scapular blade (the primitive state), gradually curving away from the blade, its margin never achieving a full 90° angle to the anterior margin of the blade (WILSON & SERENO, 1998: 45). In the derived state the expanded acromion achieves a length greater than 150% of the minimum width of the blade.

The scapulae from Peirópolis show interesting data on this character. The Table 17 shows the scored percentages of the acromion length in relation to the respective minimum width of blade in some of them (the most complete, where the most accurate measurements could have been made).

The results in Table 17 show considerably variation of the character described by WILSON & SERENO (1998). It clearly shows that the character is valid for small scapulae, but as long s they grow larger, the acromion width in relation to the minimum width of the blade achieves lower values. Nevertheless, the authors mentioned pointed out that, except for most titanosaurs, these expanded dimensions of the acromion are typical of more advanced sauropods (WILSON & SERENO, 1998: 46). Among titanosaurs, *Alamosaurus* has the broadest acromion, with an anteroposterior width approximately 150% that of the neck of the blade. Other titanosaurs have reduced the length and relative size of the acromion (e.g. *Opisthocoelicaudia* and *Saltasaurus*). This reduction is accentuated by overall expansion of the size of the coracoid in all known titanosaurs (WILSON & SERENO, 1998: 46).

The observations of WILSON & SERENO (1998) coupled with the presence of small scapulae of probably young individuals from Peirópolis (which clearly show the derived state), suggest that this character can be also ontological, gradually changing as the animal grew older.

The second character discussed by WILSON & SERENO (1998: character n° 104) refers to glenoid orientation. The glenoid is flat in most sauropods and forms a surface, which is roughly perpendicular to the base of the scapula and coracoid. In some forms, the glenoid is slightly visible laterally or medially. In all of these taxa, however, the scapular and coracoid portions of the glenoid are not offset with respect to each other. In *Euhelopus* and titanosaurs, the scapular and coracoid glenoid are offset with respect to each other, so that the scapular glenoid faces medially whereas the coracoid glenoid faces laterally. The scapular glenoid is deep mediolaterally and strongly beveled medially in *Euhelopus*, *Opisthocoelicaudia* and *Saltasaurus*. The scapular glenoid appears relatively narrow in *Titanosaurus colberti*, but is nonetheless beveled medially (WILSON & SERENO, 1998: 54).

This character is synapomorphic for the Somphospondyli, a clade comprising both *Euhelopus* and the Titanosauria.

This character is present in all scapulae of Peirópolis in which the glenoid portion has been preserved, which allows its allocation at least into the Titanosauria, since none of them shows any forward projection of the acromion, typical of the scapula of *Euhelopus* (as figured in WILSON & SERENO, 1998, fig. 18A).

The third and last character signaled by WILSON & SERENO (1998, character n° 109 – distal blade shape) was not discussed by the authors in their text. Nevertheless, they listed it in the appendix and scored it in the character-taxon matrix (WILSON & SERENO, 1998: 67-68). This character assumes two states: the scapular distal blade shape may be either not expanded (the primitive condition) or may have a rounded expansion on acromial side (the derived condition). By the character matrix provided by those authors (1998: 67), we learn that only *Camarasaurus* and the Brachiosauridae bear the derived condition. The primitive one is spread among all other sauropod taxa, including *Euhelopus* and the Titanosauridae. This is rather interesting for the present work, since the distal blades of the two largest scapulae from the Peirópolis material (MCT 1708-R and 1709-R) do bear a expansion on their acromial side, although not exactly like those of *Camarasaurus* and *Brachiosaurus*.

SALGADO, CORIA & CALVO (1997a) defined only one character for the scapula, which is: dorsal prominence on inner face of scapula (SALGADO *et al.*, 1997a, character n° 33). The presence of this prominence indicates that the character is in its derived state, and is synapomorphic for an unnamed taxon which includes the titanosaurids *Aelosaurus*, *Alamosaurus sanjuanensis*, *Neuquensaurus australis* and *Saltasaurus loricatus* (SALGADO *et. al*, 1997a: 23 – Unnamed taxon V).

All the scapulae from Peirópolis, but two (MCT 1642-R and MCT 1703-R) bear a prominence on the inner face of the blade, near its upper margin. This prominence is different from that presented by the Argentinean taxa above mentioned (personal observation). Such prominence is well developed in the Argentinean taxa, and its presence in *Alamosaurus sanjuanensis* is presumed by those authors by the analysis of available figures and descriptions (SALGADO *et al.*, 1997a: 23). The examination of *Alamosaurus sanjuanensis* is thus desirable, since its prominence may have a different morphology, shared only by the North American species and the Brazilian ones.

The last work to deal with characters of the scapula is that of SANZ *et al.* (1999). These authors have defined two characters for the scapula: presence of medial prominence close to the dorsal margin of the scapular blade (n ° 31) and presence of ridge on the ventral margin of medial side of scapular blade (n° 32).

The first character is synonymous to the just above discussed character n° 33 of SALGADO *et al.* (1997a), which is also present in *Lirainosaurus astibiae* (SANZ *et al.*, 1999: 242). The second character is defined as a ridge situated close to the ventral margin of the scapular blade, and is regarded as a diagnostic autapomorphy of this species (SANZ *et al.* 1999: 237). In fact, it is not present in any of the Peirópolis scapulae.

CORACOID

The coracoid is generally subcircular in dinosaurs but may also be rounded, rectangular or triangular is shape. A coracoid foramen, which carries the supracoracoid nerve and associated blood vessels, is situated anteroventral to the glenoid fossa, which marks the junction between scapula and coracoid. The glenoid fossa is a biplanar structure with an open articulation of 120° or greater; its articular surface is slightly concave. The glenoid appear to have been covered by a cartilaginous surface in life, allowing a wide degree of movement (PADIAN, 1997: 531).

The coracoid is the insertion point of some girdle and limb muscles (BORSUK-BIALYNICKA, 1977: fig. 6). The most important are: the *supracoracoideous* (spc), which inserts into a concave area just in front of the coracoidal foramen; and the *biceps* (bi), which inserts itself over the superior lateral border of the bone (Fig. 9).

In the Sauropoda, the large coracoid can be oval to quadrangular in shape. Its articular margin with the scapula may be nearly straight or take a noticeable deflection near the center just above the foramen. The plate is heaviest near the glenoid cavity but thins markedly forward (McINTOSH, 1990: 365).

In the Cetiosauridae Cetiosaurinae *Haplocanthosaurus*, the coracoid is subcircular (McINTOSH, 1990: 378). In the Brachiosauridae *Brachiosaurus*, the coracoid lacks the regular oval or quadrangular shape of the camarasaurids and diplodocids and has an irregular outline, the scapular border exhibiting a jog upward from rear to fore at midlength (McINTOSH, 1990: 382). In the Camarasauridae (represented by *Camarasaurus*) the coracoid is oval, its articular margin with the scapula straight. In *Euhelopus*, the coracoid is relatively small, and its border with the scapula exhibits a marked jog upward just above the coracoid foramen (McINTOSH, 1990: 387). In the Diplodocidae, the coracoid is quadrangular in *Apatosaurus* (McINTOSH: 1990: 391).

In the Titanosauridae (as *Saltasaurus*), the large quadrangular coracoid articulates further forward than in most sauropods (McINTOSH, 1990: 395). In *Malawisaurus dixeyi*, the coracoid is oval, contrasting with the quadrangular shape found in *Saltasaurus loricatus*, *Neuquensaurus australis*, probably *Alamosaurus sanjuanensis* and *Opisthocoelicaudia skarzynskii* (SALGADO *et al.* 1997a: 22).

General observations:

Six coracoids compose the material from Peirópolis (Tables 18 and 19, Fig. 12). They show different sizes, but are rather morphologically similar. The two largest coracoids (MCT 1600-R and MCT 1602-R) came from "Galga". They are almost the same size, but, unfortunately, both are left coracoids, indicating that the "Galga" material is a mixture of more than a single individual. Both bones are a little damaged.

The smallest coracoid (MCT 1653-R, left) has been recovered from "Site 1", as attested by information written on its plaster base. It is very well preserved. This coracoid fits together with the smallest left scapula, MCT 1652-R, although the contact between

them is not at all perfect. This may be due to the existence of some cartilage between the two bones in the live animal. Nevertheless, we consider herein that these two bones have belonged to the same individual.

The other three coracoids (MCT 1691-R, MCT 1703-R and MCT 1710-R) have unknown provenance, and were thus recorded as "Peirópolis surroundings". MCT 1710-R (right) is almost the same size of MCT 1602-R, and very damaged. The other two are the most important coracoids, not only for their excellent state of preservation, but because they have been found articulated with their respective scapulae.

Morphology:

The coracoids from Peirópolis are rather uniform in respect to their morphology (Fig. 25). They display the typical titanosaurid outline shape, that is, the anteromedial border (ant bd) is straight, not rounded, giving the bones a quadrangular profile (SALGADO *et al.*, 1997a; SANZ *et al.*, 1999). Due to its excellent state of preservation, and because it was found articulated with its scapula, the coracoid MCT 1703-R was the model to the general description given below.

In lateral view, the coracoid assumes a rather rhomboid shape. The anterior portion is smooth and convex. The posterior portion is dominated by a large concave fossa (conc fs), which is continuous with the fossa bore by the scapular plate. Inside this concavity, lays the coracoidal foramen (co fo). The coracoidal foramen is large, and assumes a circular to elliptical shape. Almost in all coracoids, it is placed off the scapular articular margin (sc art mg) by a distance approximately equivalent to one diameter (the exception is MCT 1600-R – see below). A suture line (st li) is visible in all coracoids, marking the point of complete closure of the coracoidal foramen.

The anterior margin of the coracoid is straight (slightly concave in MCT 1691-R), thickened, and very rugose. The superior margin is also straight, and its border is paralleled to the glenoid. The proportions of these two borders vary, however, in different coracoids (see below).

The posterior margin is the articular area for the scapular plate. It begins from the end of the superior margin, going down in a straight line until the level where the coracoid foramen is placed. This line suffers then an abruptly central deflection, forming an indentation (ind), and from that point on, it continues downwards again as a straight line.

This indentation is well marked in MCT 1653-R, MCT 1691-R and MCT 1703-R, and less marked in the other coracoids (Fig. 25 - D). The inferior margin of the coracoid may be divided in posterior and anterior portions. The posterior portion is formed by the glenoid (gl) surface, whereas the anterior portion assumes the shape of a concave curved line (conc li), which delimitates the lower corner of the anterior border of the coracoid (Fig. 25 – D).

In proximal (anterior) view, the coracoids have a more or less triangular shape, base down and apex up. The bone is plate-like, with a great expanded side, which corresponds to the glenoidal area. The medial side is straight, the lateral one gradually curves itself outside, accompanying the expansion of the glenoid. The lower margin of the glenoid is not straight, but begins from the medial side horizontally, curving upwards laterally.

In glenoidal view, the glenoid is an ample, irregular subquadrangular surface, covered by rugosities and grooves.

In distal (posterior) view, the articular scapular border begins thin at about the upper half, going down and turning progressively thick towards the glenoid area. This design matches the same design of the anterior articular border of the scapular plate. Viewed from above, the coracoid assumes a curved shape, concave medially and convex laterally. The anterior portion of the superior margin is thicker than the posterior one.

In medial view, the coracoid displays a concave surface. The most conspicuous trait is an oblique elevation (obl el), which extends itself from the upper posterior articular corner down to the center of the bone, ending just in front of the coracoidal foramen. Behind this elevation, the surface is concave (Fig. 25 – B, E).

The coracoidal foramen trespasses the coracoid plate obliquely, so that, if viewed from the lateral side, it is placed at some distance from the posterior articular margin. If viewed from the medial side, however, the coracoidal foramen is set near the same margin.

Due to the uniform morphology displayed by the coracoids, we have not recognized distance morphotypes among them. Nevertheless, they show some variation, and for that reason we have made some comments, focusing on each bone separately.

Material: MCT 1600-R, MCT 1602-R, MCT 1653-R, MCT 1691-R, MCT 1703-R, and MCT-1710-R.

MCT 1600-R (left) (Fig. 57 – C, D); MCT 1602-R (left) (Fig. 54 – A, C, D) and MCT 1710-R (right) (Fig. 57 - A): these three coracoids are the largest, and all display the

same basic morphology. The superior margins of these coracoids are shorter than the respective anterior margins, so that the bone assumes a rather irregular shape, although still quadrangular. MCT 1710-R is very damaged, but in overall shape it is similar to the other two. The scapular articular margins are broken and incomplete in all bones, so it is not possible to evaluate with certainty if these margins bear or not the posterior indentation described in the above section. The coracoidal foramina of both MCT 1602-R and MCT 1710-R are irregularly ovoid, and normally placed, that is, not distant from the scapular articular margin. The foramen of MCT 1600-R, however, is circular and placed from its articular margin at least for a distance equivalent to two diameters.

MCT 1653-R (left) (Fig. 54 – B; Fig. 57 - B): this is the smallest of all coracoids from Peirópolis. This bone is very well preserved. It shows the same general morphology of the others. Its superior border, however, is longer than its anterior border, an unique trait. But this may only reflect the fact that it belonged to a young individual. The coracoidal foramen is circular as in MCT 1600, but normally placed, that is, not distant from the scapular articular margin. This coracoid articulates loosely with scapula MCT 1652-R.

MCT 1691-R (left) (Fig. 25 – D, E; Fig. 55): this coracoid was found articulated with its respective scapula, and bears some unique features of its own. The anterior, superior and articular margins are all the same length, which gives the bone a rather symmetric, quadrangular shape. The anterior margin is straight, and projects itself anteriorly more than in other coracoids. In anterior view, it is obliquely set, so that its lower corner is medially displaced. The anterior margin is thick, the superior one is very thin. On the point where these margins converge, that is, on the superior anterior corner of the coracoidal plate, there is a small, blunt anterior protuberance (ant prt), anteriorly projected (Fig. 25 – D). This protuberance is absent from all other coracoid which have this site well preserved. The posterior articular margin bears the above mentioned indentation, placed at the same level al the coracoidal foramen. The coracoidal foramen is oval, and normally placed.

MCT 1703-R (left) (Fig. 25 – A, B, C; Fig. 56): this one has been also found articulated with its scapula. The superior margin is a bit longer than the anterior one. In the articulated scapulocoracoid, it surpasses a little the superior border of the scapular plate. The articular border bears an indentation which matches with the indentation bore by the

scapular plate. The coracoidal foramen is set from the scapulocoracoid articulation at a distance that equals its diameter. Besides, it is set far from the superior margin.

Comparisons within bones:

Although no morphotypes have been defined for the Peirópolis coracoids, it is possible to make some comments on the variation displayed within the bones.

The main variation is detected in the ratio between anterior and superior margins of the bone. The proportions of these two margins vary within different coracoids as long as they grow in size. The height of anterior border : length of superior border ratio equals 1,13 (MCT 1653-R), 1,0 (MCT 1691-R), 0,96 (MCT 1703-R) and 0,74 (MCT 1602-R). This difference of proportion may reflect only a variation caused by growth, since the largest values are found in the smallest coracoid, decreasing gradually towards the largest.

MCT 1691-R is the only coracoid to possess a protuberance on its superior anterior corner. We considered, however, that this feature was not sufficient to designate a second coracoid morphotype, for it seems to be a unique feature of this bone. New findings in the future will confirm or contradict this decision.

Comparisons with other taxa:

The Peirópolis coracoids have been compared with the following taxa: *Alamosaurus sanjuanensis*; *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Saltasaurus loricatus*; *Titanosaurus australis*; *Titanosaurus colberti*.

The left coracoid of the hypodigm of *Titanosaurus australis* (MLP/CS 1096) is fused to the scapula (HUENE, 1929: lam. 9, fig. 3) and has a more rectangular shape than the rhomboid coracoids from Peirópolis. The superior border is longer than the anterior one, a trait found only in the small MCT 1653-R. It has a sinuous margin, set continuously and at the same level as the superior margin of the scapular plate. The anterior border projects itself well anteriorly, as in MCT 1691-R, but there is no protuberance on the antero-superior corner. The coracoidal foramen is small and placed far from the scapular articular margin, as well as from the superior border. The suture line between the fused scapulocoracoid shows no trace of indentation, being rather straight.

The left coracoid of the hypodigm of *Saltasaurus loricatus* (PVL 4017-100) is similar in shape to the coracoid of *Titanosaurus australis* (POWELL, 1992: fig. 29). The anterior border is also anteriorly projected, as in MCT 1691-R. The lower border of the coracoid placed just before the glenoid, is however straight in *Saltasaurus* (as well as in *T. australis*), while it is a concave curve in all Peirópolis coracoids. The coracoidal foramen is large, and seems to be set at a longer distance from the scapular articular margin than the foramina of the Brazilian coracoids. The articular margin is not indented. By the available drawing of the coracoid of *S. loricatus* in medial view (POWELL, 1992: fig. 29B) it is not possible to confirm whether an oblique elevation is present or not in that taxon.

The left coracoid of the holotype of *Titanosaurus colberti* (ISIR335/58) is very different from the coracoids from Peirópolis. Its rectangular shape is irregular, the bone is even a little bit oval at the posterior end, the coracoidal foramen is too small, centered placed, and there is no indentation on the articular border (JAIN & BANDYOPADHYAY, 1997: fig. 19). The antero-superior corner bears no protuberance (differing from MCT 1691-R). The medial oblique elevation present in the coracoids from Peirópolis seems to be absent.

The coracoid of *Titanosaurus colberti* seems to carry a small protuberance over the middle of the superior border. A similar elevation, as well as a small coracoidal foramen, seems to be traits also present in *Titanosaurus australis*.

The coracoid of *T. colberti* is not articulated to the scapula, so it is not possible to know if its superior border surpassed the superior border of the scapular plate (as occurs in *Alamosaurus sanjuanensis* and in Brazilian MCT 1703-R).

The coracoids of the holotype of *Opisthocoelicaudia skarzynskii* (ZPAL MgD-I/48) differ from the material from Peirópolis by several aspects (BORSUK-BIALYNICKA, 1977: fig.6). Both coracoids fused to the scapulae. The anterior border of the bone is forward projected (even more than in MCT 1691-R). Both superior and inferior corners of the anterior border are pointed, the inferior one being longer. This one forms a deep concavity in the inferior margin of the coracoid, restricted posteriorly by a long glenoid expansion. The coracoidal glenoidal articular area has almost the same length of the scapular glenoid, which is wide opened (BORSUK-BIALYNICKA, 1977: fig. 6). The line of suture is not well discernible (BORSUCK-BIALYNICKA, 1977: 22), so, the presence or not of an indentation on the scapulocoracoid articulation is difficult to confirm. There is no protuberance on the antero-superior corner of the coracoid.. The superior border of the coracoid is continuous with the superior border of the scapular plate (as in Brazilian MCT 1691-R). The coracoidal

foramen is large, elliptical, and passes diagonally backward through the bone, emerging on the inner side close to the coraco-scapular suture (BORSUK-BIALYNICKA, 1977: 24). This also happens in the Brazilian coracoids.

The right coracoid of the paratype of *Lirainosaurus astibiae* (MCNA 7460) pl.5) is quadrangular in shape (SANZ *et al.*, 1999: pl.5), similar to those of Peirópolis, differing from the more rectangular shape found in other species (*Saltasaurus loricatus, Titanosaurus australis, Titanosaurus colberti and Opisthocoelicaudia skarzynskii*). The coracoidal foramen, however, is set dorsally, near the superior margin of the bone, being a unique trait of this species (SANZ *et al.* 1999: 242). The scapular articular border bears no indentation. There is no protuberance on the antero-superior corner. The coracoid of *Lirainosaurus astibiae* has been just figured in lateral view (SANZ *et al.*, 1999: pl. 5), so it is not possible to evaluate the presence of an oblique elevation on its medial surface.

The most similar to the Brazilian material is the left coracoid of *Alamosaurus sanjuanensis* (additional material USNM-15560). Its subrectangular shape matches the shape of the largest coracoids from Brazil (MCT 1600-R and MCT 1602-R). The superior border curves outside, surpassing the superior margin of the scapular plate (as in MCT 1703-R). The scapulocoracoid articulation, is so fully fused that the suture line is difficult to detect (GILMORE, 1946: 36). Nevertheless, the suture has been figured as an indented line, just like the coracoids from Peirópolis (GILMORE, 1946: fig. 6). The large elliptical coracoidal foramen passes diagonally backward through the bone, emerging on the inner side close to the coraco-scapular suture (GILMORE, 1946: 36). The same situation occurs in the Brazilian bones. The protuberance on the antero-superior corner is absent. The presence of an oblique elevation on the medial face cannot be evaluated from the available description and drawings.

Characters of the coracoid described in previous Sauropod phylogenies:

There are few characters described for the coracoid in previous sauropod Phylogenetic studies.

SALGADO *et al.* (1997a) in their analysis of Sauropod dinosaurs defined an important character for the coracoid: coracoid outline (n° 29). According to them, this character may assume two states among sauropod dinosaurs. The coracoid may be either oval (the primitive condition) or quadrangular (the derived condition). The derived condition is synapomorphic for their Unnamed Taxon II, a clade within the Titanosauridae,

which unites a group of species more closely related to the Saltasaurinae than to *Malawisaurus dixeyi* and *Epachthosaurus sciuttoi*.

Among those species listed by those authors as pertaining to the Unnamed Taxon II is the Titanosaurinae indet. DGM "B series" (a specimen made of cervical and a complete row of dorsal vertebrae, which has come from Site 1 of Price). This species was included in Taxon II only for the presence of a synapomorphy of the dorsal vertebrae, since there is no coracoid associated with this vertebral series (SALGADO *et al.*, 1997a: 22). Nevertheless, the coracoids of Peirópolis do have quadrangular shape, confirming thus their allocation within Unnamed Taxon II SALGADO *et al.*, 1997a.

The character above mentioned was redefined by SANZ *et al.* (1999) as antero-medial coracoid outline (character n° 33 of their analysis), with two character states: rounded (primitive condition) or straight (derived condition). They argued that the coracoid general outline had been defined as subquadrangular by several authors but they thought that this character was better described by using only the anteromedial coracoid outline (SANZ *et al.*, 1999: 248). According to these authors, the character is present in *Haplocanthosaurus*, *Opisthocoelicaudia*, *Saltasaurus* and *Lirainosaurus astibiae*.

SANZ *et al.* (1999) have defined another character for the sauropod coracoid: position of coracoidal foramen (SANZ *et al.*, 1999:248 - character n° 34) with 3 character states.

The coracoidal foramen may be close to scapular margin, relatively far from dorsal margin (primitive condition); far from scapular margin (derived condition) and close to scapular margin and close to dorsal margin (second derived condition). The second derived condition is a trait found in European titanosaurids such as *Lirainosaurus astibiae*, *Ampelosaurus* and *Magyarosaurus* (SANZ *et al.* 1999: 252). This condition is absent among the Peirópolis coracoids.

UPCHURCH (1995: 379) defines a character of the coracoid as "the dorsal margin of the coracoid projects above the dorsal margin of the proximal plate of the scapula". This character is one of four, which unites *Saltasaurus* and *Alamosaurus* (UPCHURCH, 1995: 379). Although this character may be accessed in only two of the coracoids from Peirópolis, which have been found articulated with their respective scapulae, it is clearly seen that one of them (MCT 1703-R) bears the character, while the other (MCT 1691-R) does not (Fig. 23).

STERNAL PLATE

The sternum is formed of two plates (typically fused in adults) and has been reported in ornithischians, saurischians and sauropodomorphs. In sauropodomorphs the sternal plates are separate and ellipsoid; the anterior en is thicker than the posterior end, which is rugose for the reception of sternal ribs (PADIAN, 1997: 534).

In the Sauropoda, the ossified sternum consists of a pair of broad plates, whose heavier ends lie forward (McINTOSH, 1990: 365).

The most important muscle to attach to the sternal plates is the *pectoralis* (p), which inserts on the lower surface of the plate, going to the deltopectoral crest of the humerus (BORSUK-BIALYNICKA, 1977: fig. 9b).

The plates vary considerably in shape and size and are particularly large in *Cetiosaurus*, *Haplocanthosaurus*, and titanosaurids. The rear edges are rugose for the attachment of cartilaginous sternal ribs, which are seldom fossilized (McINTOSH, 1990: 365).

In *Brachiosaurus brancai*, Camarasauridae, Diplodocidae, the sternal plates have an oval to irregular outline. In contrast, in *Epachthosaurus sciuttoi*, *Opisthocoelicaudia skarzynskii*, *Aelosaurus*, *Alamosaurus sanjuanensis*, and *Saltasaurus loricatus* they are semilunar in shape (SALGADO *et al.*, 1997a: 22).

General observations:

Four sternal plates have been recovered from Peirópolis deposits (Tables 20 and 21, Fig. 13).

MCT 1589-R (right) has come from "Galga" deposits. It is a large sternal plate, its lateral border is well preserved, while the medial one is very fragmented.

MCT 1690-R (left) has probably come from "Site 1". It is completely preserved. It will serve, thus, as model for the morphological description given below.

MCT 1698-R (left) has come probably from "Rodovia" deposits. It is the largest of all sternal plates. It state of conservation is similar to that of MCT 1589-R, that is, the lateral side is well preserved, the medial border is broken. Unfortunately, this bone is mounted in a plaster base, but it has been encased in it so tightly, that it was impossible to

remove it for detailed study without facing the risk of braking the entire bone into pieces. So, the description of this bone, which follows in the next section, is rather incomplete.

MCT 1713-R (right) has come from "Site 1", for it was unearthed in 1958. It is the smallest of all sternal plates, but it is complete and very well preserved.

Morphology:

The four sternal plates from Peirópolis have several traits in common. They are extremely thin laminae, dorsoventrally flattened, with a long antero-posterior extension (Fig. 26; Fig. 27). The semilunar shape is typical of the Titanosauridae (SALGADO *et al.*, 1997a: 20). The bone is divided in two surfaces: an inferior or ventral one, which faces the ground; and a superior or visceral one, which faces the internal body cavity of the living animal. The lateral border is concave, while the medial one is convex. The bone is thicker in its anterior portion, getting gradually thinner towards the rear. The lateral border is thicker than the medial one, and its surface is smooth. The medial border, in contrast, is very thin and laminar, easily broken, and irregularly shaped. From the middle backward it is marginated by rugosities, possibly for the attachment of cartilaginous sternal ribs.

The ventral surface bears a longitudinal elevation on its anterior portion. This is the antero-ventral ridge (ant vnt rdg) described by some authors (GILMORE, 1946; SANZ *et al.*,1999) and considered to be the point of insertion of the muscle *pectoralis* (HUENE, 1929: 36). In frontal view, this ridge is noticed as an elevation, asymmetrically placed, closer to the lateral border of the bone. The ridge is short in relation to the whole length of the bone, splaying itself over the first quarter of its ventral surface (Fig. 26 – B, C, E; Fig. 27).

The lateral border of the sternal plate bears a small prominence, placed on the anterior quarter of the bone, at the same level where the ventral ridge disappears. This prominence is the latero-anterior process (lat ant prc) noticed by SANZ *et al.* (1999) on the sternal plate of *Lirainosaurus astibiae*. The latero-anterior process is well discernible in lateral view as an upward projected elevation (Fig. 26 – C).

When viewed from the lateral side, the bone is strap-like, the anterior portion (which corresponds to the ventral ridge) is rectangular in outline. From the end of the ridge on, the shaft of the bone curves upwards a little, until the point where the latero-anterior

process lies. The shaft then becomes narrower and follows straight and thin until almost reaching the posterior portion the bone. There, the shaft expands itself downwards a little.

The superior or visceral surface is smooth, and a bit concave anteriorly.

In posterior view, the plate assumes the shape of a drop of water, the expanded portion corresponding to the lateral border, and the thin portion corresponding to the laminar medial border (Fig. 26 – E).

Although being so similar, the sternal plates from Peirópolis may be separated into two different morphotypes. The traits that allow the identification of this morphotypes are the frontal view profile and the overall shape of the bone.

Morphotype 1

Material: MCT 1589-R and MCT 1713-R

Description: morphotype 1 sternal plates are characterized by having a triangular frontal profile, whose apex corresponds to the antero-ventral ridge (Fig. 26 – D). These plates are also transversely narrower, being more elongated than the plates of morphotype 2.

MCT 1589-R (right) (Fig. 26; Fig. 58): this bone has come from the "Galga" site. Its lateral border is well preserved, while the medial one is very damaged. Nevertheless, the bone as a whole retains the typical semilunar shape of titanosaurid sternal plates.

This sternal plate shows minor differences in relation to MCT 1690-R. The ventral ridge is more developed, the latero-anterior process is well developed and visible in ventral view. The anterior border of the bone is straight. The posterior end of the lateral border is laterally expanded. In anterior view, the ventral ridge divides the bone in two unequal portions: the medial one is thick, and almost the same height of the ridge; the lateral portion is thinner and much shorter. This gives the bone the typical triangular profile of morphotype 1 sternal plates.

The superior or visceral surface is covered by a shallow concavity (conc), which splays itself over the anterior quarter of the bone surface. This shallow concavity is delimitated posteriorly by a low transverse ridge (trv rdg), which crosses the visceral face of the sternal plate transversally, in medial-lateral direction. When this ridge reaches the

lateral border of the bone, from that point on the latero-anterior process emerges (Fig. 26 – A).

MCT 1713-R (right) (Fig. 60): This is the smallest of all four sternal plates found in Peirópolis. The year of collecting assigned to this bone (1958) indicates that it was unearthed from "Site 1". For its small proportions, it may have belonged to a young individual.

The bone is complete and extremely well preserved. The antero-ventral ridge is present, although short. In anterior view, the bone is not "T" shaped as MCT 1690-R, but displays rather the same triangular morphology as MCT 1589-R. For that reason, it was classified as a morphotype 1 sternal plate. The transverse ridge is absent, however, and the latero-anterior process is weak, visible only in lateral view. These features may be related to the young age of this individual, since this bone is more than 25% smaller than MCT 1589.

MCT 1713-R is transversely narrower than MCT 1690-R. The width in the middle : total length ratio equals 0.41 for the first and 0.49 for the latter.

Morphotype 2:

Material: MCT 1690-R and MCT 1698-R (possibly).

Description: morphotype 2 sternal plates are characterized by having the "T" shaped frontal profile, which seems to be the normal trait in other titanosaurids (Fig. 27 – B, C). They are also relatively wider in overall shape than in morphotype 1.

MCT 1690-R (left) (Fig. 27 – A, B; Fig. 59 – A to E): this bone has come possibly from "Site 1" (*fid.* Diógenes Campos). It is completely preserved, a rare feature among these fragile and easy-broken bones. The ventral ridge of this bones is less developed than in the previous one. The anterior border of the bone is rounded, instead of straight. In frontal view, the ventral ridge assumes the shape of an asymmetrically placed elevation, which divides the anterior surface in two portions of the same thickness, the lateral one being shorter. This gives the bone a rather "T" shaped profile, typical of morphotype 2 (Fig. 27 – B). The latero-anterior process is present, although with less development than

in MCT 1589. It is not well visible in ventral view, but in lateral view it is quite discernible (Fig. 59 – C).

The superior surface is very smooth and bears a shallow concavity, although incipient. The transverse ridge is absent.

MCT 1698-R (left) (Fig. 59 - F): this bone has come probably from the "Rodovia". It is the largest of all sternal plates, and the medial border is broken. It is mounted on a plaster base, but is so tightly encased in it, that it was impossible to remove it to study its ventral surface. Nevertheless, it is possible to see that is has also a ventral ridge on its anterior portion. The latero-anterior process is less discernible, but is also present, and it shows the same development as in MCT 1690. The low transverse ridge is absent. This bone falls into morphotype 2 category.

Comparisons within morphotypes:

The existence of two sternal plates of different sizes, but with the same morphology (MCT 1589-R and 1713-R) suggests that the difference between the two morphotypes detected is real, and not the product of a ontogenetic development. Just the more developed latero-anterior process of MCT 1589-R is here considered as the result of its belonging to a larger, older individual Besides, the sternal plates of morphotype 1 are different from all other known titanosaurid sternal plates, for they are rather elongated. The sternal plates of morphotype 2 are similar in overall shape to those of other known titanosaurids.

Comparisons with other taxa:

The Peirópolis sternal plates have been compared with the following taxa: *Aelosaurus sp.*; *Alamosaurus sanjuanensis*; *Laplatasaurus araukanicus*; *Lirainosaurus astibiae*; *Malawisaurus dixeyi*; *Opisthocoelicaudia skarzynskii*; *Saltasaurus loricatus*; *Titanosaurus australis* and *Titanosaurus robustus*.

The articulated sternal plates of *Malawisaurus dixeyi* (specimens SAM - n° 89-123 and 89-124) differ not only from the Brazilian ones, but also from all other titanosaurid sternal plates, with the exception of *Alamosaurus* (JACOBS *et al.*, 1993: 527). The bones are not exactly semilunar in shape, being rather rectangular, with a slightly concave lateral

border (JACOBS *et al.*, 1993: fig. 1F). The posterior extremities are two times wider than the anterior ends, and squarely truncated as in *Alamosaurus*. The internal borders are almost straight, curving only along the anterior portion, where the two bones articulate together to form the *sternum*. The antero-ventral ridges and the latero-anterior process are both absent.

Huene identified the sternal plate attributed to *Laplatasaurus araukanicus* as a left one (HUENE, 1929: 57) but his drawings show a right sternal plate (HUENE, 1929: lam. 22, fig. 17). The right sternal plate of the hypodigm of *L. araukanicus* (MLP/CS 1322) lacks an antero-ventral ridge, as well as latero-anterior process, making it easily distinct from the bones from Peirópolis.

The holotype of *Aelosaurus rionegrinus* lacks sternal plates. The following comparison is based in two incomplete sternal plates of an additional specimen referred to the genus (MCPA-27100 – SALGADO *et al*, 1997b).

Only the right sternal plate of this specimen is figured, and it was only briefly described (SALGADO *et al.*, 1997b: fig. 3a). The only drawing available depicts the plate in ventral view. It bears neither a ventral ridge, nor a antero-lateral process. In overall shape it is not much longer than wide, resembling MCT 1690-R (morphotype 2) in this respect.

The sternal plates of the holotype of Opisthocoelicaudia skarzynskii differ from the Peirópolis ones by the absence of both an antero-ventral ridge and a latero-anterior process (BORSUK-BIALYNICKA, 1977: pl. 7, fig. 2 and pl.11, fig. 1). The bone is rather flat and the lateral curve is strongly concave, as in *Alamosaurus sanjuanensis*.

The sternal plates of *Alamosaurus sanjuanensis* (additional specimen USNM-15560) are similar to the Brazilian ones in having an antero-ventral ridge. They do not have, however, the latero-anterior process that is present in the sternal plates from Peirópolis. The anterior border of the sternal plates of *A. sanjuanensis* are curved, as in MCT 1690-R (morphotype 2), but the lateral border, however, seems to be strongly curved, being more concave than in the Brazilian bones (GILMORE, 1946: fig.5 and pl.9). The posterior border is broad and squarely truncated (GILMORE, 1946: 33), a trait not present in any of the Brazilian sternal plates.

The pair of incomplete sternal plates attributed to *Titanosaurus australis* (hypodigm MLP/CS 1260 and MLP/CS 1104) are similar to the sternal plates from Peirópolis in having an antero-ventral ridge (HUENE, 1929: lam 9, figs. 1 and 2). This ridge seems

more well developed in this species, extending itself over more than the first quarter of the bone, and its anterior border is enlarged in MLP/CS 1104 (HUENE, 1929: lam. 9, fig. 2a and c), a trait not present in the Brazilian material. The anterior border of the plate of *T. australis* is a little squared, as in MCT 1589-R (morphotype 1), but because the medial border is broken and lost, its is impossible to tell if the bone is equally elongated. Nevertheless, the most similar feature that *T. australis* shares with the Brazilian material is the "T" shaped proximal profile, a trait present in morphotype 2 sternal plates (HUENE, 1929: lam 9, fig. 2c). A feature that however distinguishes *T. australis* from both Brazilian morphotypes is the absence of the latero-anterior process (HUENE, 1929: lam. 9, fig. 2b).

A left sternal plate was attributed by Huene (1929) to *Titanosaurus robustus* (HUENE, 1929: 49) but his drawings show a right sternal plate (HUENE, 1929: lam. 18, fig.1). The sternal plate of *T. robustus* (hypodigm MLP/CS 1295) is very similar to the Brazilian sternal plates, particularly MCT 1690-R (morphotype 2). It also bears an antero-ventral ridge, which is similar in shape and proportions to the ridges bore by the Brazilian bones. Its anterior border is not squared, but oval, and also assumes a "T" shaped profile in anterior view, similar to MCT 1690-R (morphotype 2). The ventral ridge is not anteriorly enlarged, as in *T. australis*. The presence of a latero-anterior process in *T. robustus* cannot be evaluated by available drawings (HUENE, 1929: lam 18, fig 1). This process, if ever present, could be more ventrally orientated as in MCT 1690-R, being visible only in lateral view.

The left sternal plate of the hypodigm of *Saltasaurus loricatus* (PVL 4017-102) is similar to the sternal plates from Peirópolis in having an antero-ventral ridge over its ventral surface. This ridge, however, seem to be placed closer to the lateral margin of the plate in *Saltasaurus* than in the Brazilian bones (POWELL, 1992: fig. 30b). The latero-anterior process is absent from the sternal plate of the Argentinean taxon, however. In overall shape, the plate is not elongated, resembling morphotype 2. It is not possible to tell by the available drawings (POWELL, 1992: fig. 30) whether the anterior profile of *S. loricatus* sternal plates was triangular or "T" shaped.

The sternal plate that shows the greatest similarities to the Brazilian material is that of *Lirainosaurus astibiae* (paratype MCNA 7461). Although incomplete, this is the only sternal plate to display both an antero-ventral ridge and a latero-anterior process, which are similar to those present in the Peirópolis sternal plates. The antero-ventral ridge seems to be more developed than in the Brazilian bones, but by the given figures it is not possible to

know whether the proximal profile of the bone is triangular or "T" shaped. (SANZ *et al.*, 1999: pl.5). A wide depression appears on the internal side of the plate (SANZ *et al.*, 1999: 242), a trait that is perhaps equivalent to the shallow concavity present in MCT 1589-R (Fig.StPl1–A), suggesting that the sternal plate of *L. astibiae* could be elongated, as in morphotype 1. The presence of a latero-anterior process in the sternal plates from Peirópolis discards its use as an autapomorphy of *Lirainosaurus*, as stated before (SANZ *et al.*, 1999: 238).

Characters of the sternal plate described in previous Sauropod phylogenies:

There are just a few characters described in the literature for the sternal plates.

SALGADO, CORIA & CALVO (1997a) described only one character in their phylogenetic analysis of the Sauropoda: sternal plate shape (SALGADO *et al.*, 1997a, character nº 26), with two character states, suboval (the primitive condition) or semilunar (the derived condition). The derived condition is synapomorphic to the Titanosauridae level (SALGADO *et al.*, 1997a: 20). The sternal plates of Peirópolis are also semilunar, which allows their allocation into the Titanosauridae clade.

SANZ *et al.* (1999) improved the study of sternal plate morphology a little further by adding two more characters to the list: presence of lateroanterior process on sternal plate (SANZ *et al.*, 1999, character n° 29), and presence of an antero-ventral ridge of sternal plate (SANZ *et al.*, 1999, character n° 30).

The first character is defined as a visible latero-anterior prominence set on the external face of the sternal plate (SANZ *et al.*, 1999: 242). It is regarded as an autapomorphy of *Lirainosaurus astibiae* (SANZ *et al.* 1999: 237 – *diagnosis*). This character, surprisingly, is also present in the sternal plates from Peirópolis.

The second character is widespread among titanosaurian taxa. According to those authors, an antero-ventral ridge is present on the sternal plates of *Saltasaurus*, *Epachthosaurus and Lirainosaurus*. These three taxa were lumped together with *Argyrosaurus* and the "Peirópolis titanosaur" in a clade named Titanosauroidea (SANZ *et al.*, 1999: 252 – clade n° 2). They did not considered the character as a synapomorphy of the group, because it is unknown in the two last taxa. However, the sternal plates of Peirópolis do have an antero-ventral ridge. Their association with the set of vertebrae, which has been called the "Peirópolis titanosaur", is not certain yet. Nevertheless, the presence of this

character in the Brazilian material seems to reinforce the phylogenetic hypothesis presented by SANZ *et al.* (1999: fig. 4).

HUMERUS

In the Sauropoda the humerus is straight and expanded at both ends (usually more at the proximal). It always exceeds the radius and ulna in length. A prominent deltopectoral crest occupies the upper half of the lateral edge of the cranial face. The less expanded distal end exhibits small but distinct radial and ulnar condyles on its cranial side and a broad olecranon groove on the caudal one (McINTOSH, 1990: 367). The humerus is the site of attachment of several important muscles (BORSUK-BIALYNICKA, 1977: fig.7). The deltopectoral crest receives two important muscles: the *pectoralis* (p) onto the crest itself; and the scapular *deltoid* (dsc) on its lateral side. Just below the crest, the *brachialis inferior* (bri) makes its insertion on the humerus. The head of the humerus is a concave surface, which houses the *coracobrachialis brevis* (cbb) a muscle that binds the humerus to the coracoid. Two more muscles that come from the scapulocoracoid and insert into the superior margin of the humerus are the *subcoracoscapularis* (sbsc - medially) and the *supracoracoideus* (spc - laterally). The posterior surface of the humerus receives more three muscles. The *triceps* (tric) humeric heads insert medially and laterally on the head of the bone, flanking the glenoidal condyle. Far below, at about the middle of the shaft and near the lateral margin, rugose areas mark the insertion zones of the *scapulohumeralis anterior* (scha) and the *latissimus dorsi* (ld – placed just below). The distal lateral end of the humerus still bears insertion zones for three muscles which move different parts of the lower arm: the *extensor carpi radialis* (ecr), the *extensor carpi ulnaris* and the *extensor digitalis communis* (edc). All these muscles are shown in Fig. 9.

The length of the forelimb and its overall robustness vary within the Sauropoda.

Among primitive sauropods, the forelimbs of *Cetiosaurus* are of moderate length (humerus:femur ratio = 0.80) and robustness, being more robust than in *Shunosaurus*, *Barapasaurus*, *Diplodocus* and *Brachiosaurus*, just a bit more than in *Camarasaurus*, but less than in *Apatosaurus*, *Opisthocoelicaudia*, or *Saltasaurus* (McINTOSH, 1990: 377). The forelimb of *Shunosaurus* is relatively short (humerus:femur ratio = 0.62) (McINTOSH, 1990: 379).

Also short, and slender, are the forelimbs of the Diplodocinae diplodocids, such as *Diplodocus* (humerus:fermur ratio = 0.65) and *Barosaurus* (humerus:femur ratio = 0.72) (McINTOSH, 1990: 389-390). In *Apatosaurus*, however, the forelimb is still shorter (humerus:femur ratio = 0.64) and more robust (McINTOSH, 1990:391). In *Dicraeosaurus* (Dicraeosaurinae), the forelimb was also short (humerus:femur ratio = 0.62), but the humerus was stouter than those of other sauropods except *Apatosaurus*, *Opisthocoelicaudia*, and *Saltasaurus* (McINTOSH, 1990: 392).

In *Brachiosaurus* (Brachiosauridae) the forelimb is greatly elongated, and the bones are very long and slender, particularly the humerus, which is longer than the femur (humerus:femur ratio = 0.9 to 1.05) (McINTOSH, 1990: 382).

In *Camarasaurus* (Camarasauridae) the forelimb is relatively longer than those of diplodocids, but shorter than those of *Omeisaurus*, *Euhelopus* and brachiosaurids (the humerus:femur length ratio is about 0.76). The bones of the forelimb are more robust than those of *Brachiosaurus* and *Diplodocus*, but much more slender than those of *Apatosaurus* and *Opisthocoelicaudia* (McINTOSH, 1990: 385).

The humerus of *Chubutisaurus insignis* (Titanosauriform) is long and relatively slender, its proximal end squared. The humerus:femur length ratio is 0.85 (McINTOSH, 1990: 384).

Among the Titanosauridae, the forelimb is shorter than in the Camarasauridae. The humerus:femur ratio is 0.74 in *Titanosaurus indicus* is 0.74 (McINTOSH, 1990: 395), and 0.72 in *Opisthocoelicaudia* (McINTOSH, 1990: 388). The humeri of *Saltasaurus* and *Opisthocoelicaudia* are robust. In *Laplatasaurus*, the humerus is rather stout and greatly expanded at both ends (McINTOSH, 1990: 396). The humerus of *Argyrosaurus* is relatively robust with a squared proximal end reminiscent of *Saltasaurus* and *Opisthocoelicaudia*, but the incomplete humerus of *Antarctosaurus* appears to be slender (McINTOSH, 1990: 397).

General observations:

There are six humeri available for study (Tables 22 and 23, Fig. 14). Five of them come from the three main sites, with the exception of MCT 547-R . It was collected somewhere in Uberaba, a city close to Peirópolis. Although only the proximal half of the

bone has been preserved, it is such a good state of preservation (specially in relation to the prominence over the deltopectoral crest) that we decided to include it in this study.

The humeri are all very similar to each other, varying in size (Fig. 65 – D to H). Its impossible to detect any morphological differences to support their segregation in different morphological categories, except for a slightly variation in overall robustness.

The most part are slender type humeri, while the only humerus from "Galga" (MCT 1597-R) is somewhat more robust than the others. This is a large and heavy bone, with many signs of erosion in both extremities.

Two of the humeri have come from "Site 1" deposits: MCT 1674-R and MCT 1688-R. MCT 1674-R is the smallest humerus from Peirópolis. The site of origin (Site 1) was recognized thanks to a photography taken by L.I.Price, on where he wrote some notes about its dimensions and its site of origin. MCT 1688-R is the largest of all humeri from Peirópolis.

The last two humeri (MCT 1682-R and MCT 1684-R) were scored as "Peirópolis surroundings". MCT 1682-R bears a inscription – DGM 811-LE – which may help clarify its origins. It is one of the largest humeri (almost the same size as MCT 1688-R), but displays the same morphology as the others.

Morphology

The humeri of Peirópolis are all morphologically similar, and it was not possible to separate them into distinct morphotypes.

The humerus has a straight shaft with both ends unevenly expanded, constricted in the middle. Its cross-section it is elliptical, the longest axis is the medial-lateral one (Fig. 28).

In anterior view, the lateral margin of the bone is slightly concave, the curvature is almost straight in its upper half. The medial margin is strongly concave, with a well discernible curvature up and down.

The head of the humerus is asymmetrically expanded. It extends itself until the middle of the shaft and has an inverted triangular outline, the medial border is more developed than the lateral one. The head is strongly concave, resembling a spoon. In some humeri, the concavity bears still another concavity, more or less rectangular in shape, and placed over the superior medial corner. This second concavity houses the muscle *coracobrachialis brevis* (BORSUCK-BIALYNICKA, 1977: fig. 7) (Fig. 28 – A, B).

The lateral border of the head of the humerus is dominated by the deltopectoral crest (dp cr). This crest is well developed in all humeri (Fig. 28 – B; Fig. 29 – A). It is forward and a little bit medially projected. It begins near the latero-superior corner of the humerus as a laminated structure, descending along the lateral border of the head, gradually swelling downwards. Then it merges into the shaft, just at the base of the humerus head. In all humeri in which the deltopectoral crest is well preserved (particularly MCT 547-R and MCT 1684-R), there is a laminar longitudinal prominence (lng prm) on it (a character also present in *Aelosaurus rionegrimus* – see below) (Fig. 29).

The medial border of the humeral head is very developed, and well projected medially. It is not pointed, but has a truncate end, delimited by an almost vertical margin. This border is thick and curves itself a little anteriorly and has a flat triangular surface.

The superior border of the humerus head is horizontally straight, and marked by parallel groves along its length. This straight superior margin sided by the truncated medial border plus the straight orientation of the deltopectoral crest give the humeral head a rather squared outline, well distinct from the racket-shaped humeri of other non-titanosaurian sauropod dinosaurs.

Still in anterior view, the distal portion of the humerus is also expanded, but to a lesser degree than the proximal one. It dominates the distal third of the bone, and is symmetrically expanded both medially and laterally. The inferior margin of the distal portion is straight. The surface is occupied by a longitudinal convex elevation, sided by two longitudinal concavities. The convex elevation is not set at the mid-line of the shaft, but is rather displaced laterally. The medial longitudinal concavity is thus wider than the lateral one and faces forward. The other is narrower and faces a little laterally.

In posterior view the bone shows the same general outline as in anterior view, with minor details. The posterior surface of the head is convex, the glenoidal condyle (gl cnd) that fits into the glenoid is clearly noted as a rounded structure on the summit of the bone (Fig. 28 – C, D). The lateral border of the humeral head shows a swelling, which corresponds, to the insertion of the muscle *scapulohumeralis anterior* (BORSUK-BIALYNICKA, 1977: fig. 7). The distal third of the shaft bears two well developed divergent crests, which correspond to the posterior supracondylar ridges (pos cnd rdg) discussed in the next section. The presence of this character in all Peirópolis humeri allows their allocation in the Titanosauroidea *sensu* Upchurch (SANZ *et al.* 1999). The two ridges are placed symmetrically over the distal surface of the shaft. They begin together at about the upper distal third of the bone, diverging

quickly from each other and descending laterally and medially until reaching the inferior margin of the bone. The two supracondylar ridges delimit a deep, triangular concavity. The lateral ridge ends at the radial condyle (rd cnd), and the medial one ends at the ulnar condyle (ul cnd) (Fig. 28 – C, E).

In lateral view it is possible to notice that the shaft of the humerus is a little twisted, the head of the bone faces a little outwards, while the distal portion faces a bit inwards. The most conspicuous structures seen in this view are the deltopectoral crest, the glenoidal condyle and a posterior elevation, placed at the base of the humeral head (Fig. 28 – C – m. ld). The deltopectoral crest gives the head of the humerus a somewhat antero-posteriorly expanded profile. The upper border of the crest is convex, and bears a laminar longitudinal prominence. The superior margin of the prominence rises gradually from the floor of the deltopectoral crest, follows a convex curve, then merges abruptly into the crest, disappearing. The glenoidal condyle projects itself backward from the superior posterior margin of the head. It is rounded and marked by longitudinal grooves. The posterior elevation is smooth and may be the insertion area for the attachment of the muscle *latissimus dorsi* (BORSUK-BIALYNICKA, 1977, fig. 7) (Fig. 28 – C – m. ld).

In proximal view the humeral head assumes a plate like profile, and is very thick. The medial half is thicker than the lateral side. The glenoidal condyle is very conspicuous and detaches itself from the posterior margin of the humerus as a large, rounded prominence. It is not place at the middle, but dislodged a bit medially. The distal surface is covered by rugosities and surrounded by deep grooves. In distal view, the deltopectoral crest and its longitudinal prominence are quite visible.

In distal view the bone shows a rather irregular trapezoid shape. The anterior margin of this trapeze has the longest length, and bears a semicircular convex elevation (cvx el) laterally and a shallow concavity medially (Fig. 28 – E). The lateral and medial margins are a bit convex and converge gradually towards the posterior margin. The lateral one is shorter than the medial and less inclined also. The posterior margin is shorter than the anterior and strongly concave. The concavity is sided by both posterior condyles, which are well visible in distal view. The distal surface is rugose and marked by grooves. The grooves give both anterior and medial margins a crenellated pattern. The posterior and lateral margins are smooth.

The humeri from Peirópolis are rather conservative and homogeneous in their shape. It is difficult to distinguish them from each other or even find morphological

characters of their own. The above general description serves to any of the bones. Just minor information is given below.

Material: MCT 547-R; MCT 1597-R; MCT 1674-R, MCT 1682-R; MCT 1684-R and MCT 1688-R.

MCT 547-R (Right) (Fig. 29; Fig. 61): This is a large bone, in which some muscle scars are particularly strong. One of them is the *coracobrachialis brevis* fossa, on the anterior surface of the humeral head. The lateral bulge for the *scapulohumeralis anterior* is also well developed. The distal border is thick, the glenoidal condyle and the deltopectoral crest are strongly developed. The longitudinal prominence over the later is completely preserved.

MCT 1597-R (Right) (Fig. 65 – B, C): the superior margin is not straight as in normal humeri, but is slightly elevated near the medial border. The fossa for the *coracobrachialis brevis* is shallow, marked by a rugose elevation. The lateral border of the head is more expanded than in other humeri. The humeral head has different proportions than in other humeri, being more than 50% the length of the whole bone (the height of humerus head : total length = 0.52). This ratio is smaller in other humeri (it is 0.39 in MCT 1674; and 0.42 in MCT 1684), whose heads correspond to 40% of total humeral length. The deltopectoral crest is broken, so it is not possible to evaluate the presence of the longitudinal elevation seen in other bones.

MCT 1674-R (Left) (Fig. 28; Fig. 62): this is a rather slender bone, but it displays the usual morphology of all other humeri. The longitudinal elevation of the deltopectoral crest is broken, except for a little bit of it, which is sufficient to attest its presence in this bone.

MCT 1682-R (Left) (Fig. 63): its height of humeral head:total length ratio is 0.47, a bit higher than in MCT 1674-R and MCT 1684-R, but still lesser than in MCT 1597-R. The anterior surface of the deltopectoral crest bear a broken mark, suggesting the presence of the longitudinal prominence.

MCT 1684-R (Right) (Fig. 64): the prominence over the deltopectoral crest is completely preserved, but has a somewhat different shape from that present in MCT 547-R. In lateral view, this prominence arises abruptly from the floor of the deltopectoral crest, runs parallel to it for a short distance, and then merges suddenly into the bone again. That

is, this prominence has a rectangular shape in MCT 1684-R, while in MCT 547-R it has a water drop-like shape.

MCT 1688-R (Right) (Fig. 65 - A): its morphology does not differ from the usual patterns. The prominence over the deltopectoral crest in present, although a little eroded.

Comparisons within bones:

The humeri of Peirópolis are very conservative in morphology, so that we were not able to identify enough morphological variation that would support their segregation in any different morphotypes. This may have two meanings. Either the totality of Peirópolis humeri actually had the same morphology, or any different morphotype has been not preserved in the sample. The discovery of new material in the future will clarify the humerus problem.

Comparisons with other taxa:

The Peirópolis humeri have been compared with the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Alamosaurus sanjuanensis*; *Andesaurus delgadoi*; *Antarctosaurus brasiliensis*; *Antarctosaurus wichmannianus*; *Argyrosaurus superbus*; *Argyrosaurus sp.*; *Chubutisaurus insignis*; *Gondwanatitan faustoi*; *Laplatasaurus araukanicus* (=*Titanosaurus araukanicus*); *Laplatasaurus sp. (=Antarctosaurus sp.)*; *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Saltasaurus loricatus*; *Titanosaurinae from Guararapes*; *Titanosaurus australis* (=*Neuquensaurus australis*); *Titanosaurus colberti*; *Titanosaurus robustus (=Neuquensaurus robustus)*.

There are several species that may be distinguished promptly from the humeri from Peirópolis by the overall shape of the bone. Some species (*Saltasaurus loricatus*, *Titanosaurus australis*, *Titanosaurus robustus* and *Opisthocoelicaudia skarzynskii*) are characterized by a stocky, broad-headed humerus, while others (e.g. *Titanosaurus colberti*) show a more slender shaft, with a small humeral head.

The figured humerus of *Titanosaurus colberti* (holotype ISIR335/59) is a right one (JAIN & BANDYOPADHYAY, 1997: figs. 20-21), and it is different from all other titanosaurid humeri know: the proximal and distal ends are roughly of equal dimensions (JAIN & BANDYOPADHYAY, 1997: 122). The humeral head is also shorter than in all

other titanosaurid humeri, making one third of the total length (JAIN & BANDYOPADHYAY, 1977: 122). In other humeri, it makes from 40 to 50% of the total length. The deltopectoral crest is short and wide, and bears no longitudinal prominence over it. The lateral border of the head is also thickened. The upper margin of the humeral head is not straight as in the South American taxa, but convex.

The right humerus of *Titanosaurus australis* (hypodigm MLP/CS 1099) show several differences if compared with the humeri from Peirópolis. The deltopectoral crest extends itself down the shaft of the bone for more than 50% of its total length (HUENE, 1929: lam.10, fig.1). It is more robust, and lacks a longitudinal prominence. In posterior view, the lateral margin of the deltopectoral crest is sinuous, showing two convex elevations, an upper (which may correspond to the insertion point of the muscle *scapulohumeralis anterior*) and a lower, less developed one (HUENE, 1929: lam.10, fig.1b). Between the two elevations lies a shallow concavity. This trait is not present in any of the Brazilian humeri. In distal view, the humerus of *T. australis* presents a different profile too (HUENE, 1929: lam.10, fig.1d). The medial border is shorter than the lateral one (contrary to the bones from Peirópolis). The lateral border is not curved, but has a protuberant angle.

The right humerus of *Titanosaurus robustus,* of which only the proximal half was preserved, may not belong to it (HUENE, 1929: 38). We have examined the bone (MLP/CS 1019) at the Museum of La Plata (Argentina). The rugose deltopectoral crest lacks a longitudinal prominence and it is not laminar and twisted medially as in the bones from Peirópolis, being very robust instead (HUENE, 1929: lam. 18, fig.2). The scar for the *coracobrachialis brevis* is placed lower, closer to the convergence of the borders of the head.

The humerus of *Saltasaurus loricatus* (hypodigm PVL 4017-67) is a robust, short bone, whose upper margin is rather sigmoid, the medial half being convex, and the lateral one squared, just over the deltopectoral crest (POWELL, 1992: fig. 31). The deltopectoral crest is low and lacks a longitudinal prominence. The insertion zone for the muscle *coracobrachialis brevis* is similar to those of the Brazilian humeri. The lateral border of the humeral head is strongly developed and convex, more than in the humeri from Peirópolis. The distal end of the humerus of *Saltasaurus* is more expanded medio-laterally, and anteriorly deflected (POWELL, 1992: fig. 31 b).

The humerus of *Opisthocoelicaudia skarzynskii* (holotype ZPAL MgD-I/48) may be easily differentiated from the Brazilian ones by several traits. The humeral head of *O. skarzynskii* is squared, but its upper margin is not horizontal as in the Peirópolis humeri, being rather inclined, ascending in medial direction (BORSUK-BIALYNICKA, 1977: fig. 7b). It is very wide and its medio-lateral dimension makes more than 50% of the total length of the bone (BORSUK-BIALYNICKA, 1977: 26 – table 8). The deltopectoral crest is well developed, strongly turned medially, and descends down to the middle of the shaft, making the bone more robust in overall shape than the Brazilian ones. In posterior view, the bulged lateral border of the humeral head – place for the attachment of the muscle *scapulohumeralis anterior* (BORSUK-BIALYNICKA, 1977: fig. 7d) is also more developed, being similar to that of *Saltasaurus*. The glenoidal condyle is also more developed in *O. skarzynskii*, and more backward projected than in the bones from Peirópolis (BORSUK-BIALYNICKA, 1977: fig. 7c).

There are several South American taxa whose humeri are too much incomplete to allow good comparisons. Among them are *Andesaurus delgadoi*, *Laplatasaurus araukanicus*, *Antarctosaurus wichmannianus* (Argentina), *Antarctosaurus brasiliensis* and the Titanosaurinae from Guararapes (state of São Paulo), from Brazil.

The right humerus of *Andesaurus delgadoi* (holotype MUCPv 132) has been partially preserved. The distal part is represented by bone, whereas the proximal one was preserved as a natural cast, from which a replica has been made (CALVO & BONAPARTE, 1991: 307). The reconstructed bone shows a more slender outline than the humeri from Peirópolis (CALVO & BONAPARTE, 1991: fig. 8a).

The humeri of *Laplatasaurus araukanicus* are incomplete. Comparisons based on the preserved proximal and distal parts (hypodigms MLP/Av. 2052 and MLP/CS 1021) indicate that the bone were different from the stocky humeri of the Saltasaurinae (HUENE, 1929: lam. 23, figs. 3 and 4), being most similar to the slender humeri from Peirópolis. The deltopectoral crest seems to be of similar morphology, but it is not possible to attest the existence or not of a longitudinal prominence over it.

An additional humerus (PVL-3670-1) referred as *Laplatasaurus sp.* lacks both proximal and distal ends (POWELL, 1979: fig.3a). The preserved portion of the shaft has a curved medial border and a straight lateral one, and the posterior condyles are well developed (POWELL, 1979: 195). These traits, however, are usually present in all titanosaurid humeri.

The incomplete right humerus of *Antarctosaurus wichmannianus* (holotype MACN 6904) resembles the humeri from Peirópolis by being slender and by the shape of its deltopectoral crest (HUENE, 1929: lam. 32, fig. 1). The longitudinal prominence is absent, however.

Other reported Titanosauridae remains found in Brazil comprise *Antarctosaurus brasiliensis* (ARID & VIZOTTO, 1971) and a Titanosaurinae from Guararapes (state of São Paulo) (LEONARDI & DUSZCZAK, 1977). Of the later, only part of the mid-portion of the left humerus containing the base of the humeral head is preserved (LEONARDI & DUSZCZAK, 1977: figs. 2 and 3). The bone is too much fragmented to allow good comparisons with the Peirópolis humeri. Its estimated size (992mm) surpasses the largest humerus found in the DNPM/RJ collections (LEONARDI & DUSZCZAK, 1977: 401).

The remains of *Antarctosaurus brasiliensis* are restricted to the proximal half of a right humerus (GP-RD-3). With an estimated total length of 95 cm (ARID & VIZOTTO, 1971: table 2), it also surpasses the largest humerus of Peirópolis (MCT 1682-R). The deltopectoral crest is well developed and medially twisted. The presence of a longitudinal prominence cannot be confirmed by the given figures (ARID & VIZOTTO, 1971: figs. 4 and 5). The upper margin of the humeral crest is straight and horizontally set, giving the bone a squared profile similar to the bones from Peirópolis. In posterior view, two well marked rugosities were identified as the insertion marks of the muscles *scapulohumeralis anterior* and *brachialis inferior* (ARID & VIZOTTO, 1971: 300). The glenoidal condyle is rounded and well developed.

Certain species show some similarities with the Peirópolis material.

The humerus of *Chubutisaurus insignis* (holotype MACN 18222) is similar to the Peirópolis material in having the lateral corner of the humeral head rather quadrangular in shape, instead of curved, a trait which is also present in titanosaurids, *Brachiosaurus*, *Pleurocoelus* and *Bothriospondylus madagascariensis* (SALGADO, 1993: 266 and fig. 4b). *C. insignis* differs from the humeri from Peirópolis, however, in having the superior margin of the humeral head inclined, ascending in medial direction, while this margin in the humeri from Peirópolis is rather horizontal. The proportions of the humeral head in relation to the shaft are also different. According to measurements made by CORRO (1975: 235) the proximal width:total length ratio is 0.24 in *C. insignis*. This ratio is higher in all Peirópolis humeri (0.40 in MCT 1597; 0.38 in MCT 1674; 0.41 in MCT 1684 and 0.39 in MCT 1682). The humerus:femur ratio is 0.86 in *C. insignis* (SALGADO, 1993:

266), but this ratio cannot be calculated with certainty in the Brazilian disarticulated material.

The right humerus of *Alamosaurus sanjuanensis* (additional material USNM-15560) is similar to humeri from Peirópolis in being slender shaped, with a concave medial margin opposed to a rather straight lateral one. The humeral head, although broken medially, is clearly less wide than 50% of the total length of the bone (GILMORE, 1946: fig. 8). Its superior border is straight. It differs from the Brazilian material by its upper margin, which is not horizontal, but inclined, ascending in medial direction (as in *Chubutisaurus*). The deltopectoral crest is well developed, descends well down to the middle of the shaft, and bears no longitudinal prominence over it.

The left humerus of *Argyrosaurus superbus* (holotype MLP.77-V-29-1) is similar to the other humeri from Peirópolis in having straight superior and lateral margins, giving the humeral head a squared profile. The deltopectoral crest is not so robust as in *T. australis*, being more similar to the Brazilian bones. The drawings from HUENE (1929: lam. 37, fig. 1 a, b) and our personal observations (at Museo de La Plata), suggest that a prominence could have been present over it. The left humerus of an additional specimen of *Argyrosaurus sp.* (PVL 4628) resembles the humeri from Peirópolis in having a quadrangular head, but the shaft is more robust, and the distal end seems more transversally expanded (BONAPARTE, 1996: fig. 43, b, c).

Among known slender-humerus titanosaurids known so far, *Aelosaurus sp.* *Gondwanatitan faustoi* and *Lirainosaurus astibiae* are the most similar to the Peirópolis bones in the proportions of the humeral head in respect to total length.

The humerus of *Aelosaurus rionegrinus* was never figured. The following comparison was based on some photographs of the right humerus of the holotype (MJG-R1) taken by on of the authors (A. Kellner). A great portion of the bone has been not preserved (the medial side of the head), but the rest of the bone is in good shape. The lateral side of the humeral head is squared as in the humeri from Peirópolis. In overall shape the bone is a bit more robust. The shaft is wider in the middle than in the Brazilian bones, but this character may be related to size, since the humerus of *Aelosaurus* is at least 20% larger than MCT 1682-R, which is the largest humerus from Peirópolis. The deltopectoral crest is similar in shape, bearing also a prominence. This prominence seems to be also thicker than that found in Brazilian humeri. There is an additional left humerus (MPCA-27100) referred to this genus (SALGADO, CORIA & CALVO, 1997b: fig. 3b).

We have seen the specimen during a visit to Argentina. The humerus of *Aelosaurus sp.* is robust, having a wider shaft than the humeri from Peirópolis. Both medial and lateral margins are concave, due to the extremely developed expansion of the proximal portion (SALGADO *et al.* 1997b: 46). The deltopectoral crest is well developed, but there is no longitudinal prominence over it. In proximal view, the superior margin of the head is more slender, and the glenoidal condyle is less developed, distinguishing it from the Brazilian humeri. The distal part is broken and lost.

The humeri of *Gondwanatitan faustoi* (holotype MN 4111-V) have come from deposits of the Bauru Group (KELLNER & AZEVEDO, 1999: 134), which is the same stratigraphic unit where the material of Peirópolis has been found. They display the same morphology: they are slender and have a medially twisted deltopectoral crest (KELLNER & AZEVEDO, 1999: fig. 20). It is probable that *G. faustoi* may have been one of the sauropods represented in the Peirópolis fauna. The presence of a longitudinal prominence over the deltopectoral crest of *G. faustoi* cannot be confirmed, however, because its surface is poorly preserved.

The humeri of *Lirainosaurus astibiae* (paratypes MCNA 7462 and MACN 7463) also resemble the humeri from Peirópolis (SANZ *et al.*, 1999: pl. 4 a, b). The width of the humeral head is less than 50% of the total length of the bone, as in the Brazilian bones (differing from the more stocky humeri of *Saltasaurus* and *Opisthocoelicaudia*). The shaft is also well constricted in the middle, giving the bone a slender shape. The humeral head does not stretch itself below the mid-length of the shaft. Its upper margin is also straight and horizontally placed. The deltopectoral crest is curved medially, but the presence of a longitudinal prominence over it cannot be confirmed by the analysis of the given figures. There is a clearly defined scar for the insertion of the muscle *pectoralis* (SANZ *et al.* 1999: 242), but it is not certain if it is the same trait.

Characters of the humerus described in previous Sauropod phylogenies:

Although being an important bone of the forearm, the humerus has received less attention in previous phylogenic studies. There are only three characters described in the literature concerning the humerus alone.

WILSON & SERENO (1998) defined only one character for the humerus: deltopectoral attachment development (WILSON & SERENO, 1998, character n° 3).

According to these authors, prosauropods and most theropods have prominent, hatched-shaped deltopectoral crests that project anterolaterally from the shaft of the humerus, which corresponds to the primitive state of the character (WILSON & SERENO, 1998: 25). Sauropods, in contrast, bear the derived state, in which the deltopectoral crest is developed only as a low rugose ridge, with the exception of the Brachiosauridae (WILSON & SERENO, 1998: 25).

The humeri from Peirópolis display the typical sauropod crest, as described by those authors. Unfortunately, the presence of this character in the Brazilian material allows its allocation within the Sauropoda only, and is not useful at higher phylogenetic levels.

SANZ and coworkers (1999) defined two characters concerning the humerus: deltopectoral crest of humerus developed and medially twisted (character n° 35) and development of posterior supracondylar ridges on the humerus (character n° 36).

The first character is similar to that defined by WILSON & SERENO (1998), but, against those authors, presumes that the deltopectoral crest may have different degrees of development and vary within the Sauropoda. A poorly developed deltopectoral crest is thus present in "cetiosaurid" genera such as *Patagosaurus* and *Omeisaurus* (SANZ *et al.* 1999: 248) representing the primitive condition of the character. The derived condition, that is, presence a developed and medially twisted deltopectoral crest on humerus, is one of several synapomorphies supporting the Clade 2 of SANZ *et al.* (= Titanosauroidea *sensu* UPCHURCH, 1995), although these authors recognize that this feature could eventually be synapomorphic below Clade 2 (SANZ *et al.*, 1999: 252).

The other character described by SANZ *et al.* (1999: character n° 36) refers to the development of the posterior supracondylar ridges on the humerus, which may be either incipient (the primitive condition) or prominent (the derived condition). According to these authors, the derived condition is present in their Clade 2, but, as occurred with the previous character, it may be synapomorphic below this level (SANZ *et al.* 1999: 252).

Both characters above defined were scored as unknown for the "Peirópolis titanosaur" (SANZ *et al.*, 1999: 248 - data-matrix). Nevertheless, they are both present in the humeri from Peirópolis, although none of them may be associated with certainty to the vertebral sequence known as the "Peirópolis titanosaur".

ULNA

In dinosaurs in general, the ulna is stronger than the radius, which is no more than equal to it in stoutness. The olecranon is generally little developed, and may appear in secondarily quadruped ornithischian dinosaurs (ROMER, 1956: 372). In sauropods, the forelimb bones are massive. The ulna is slightly longer than the radius. The two bones are nearly straight but very slightly bowed cranially (McINTOSH, 1990: 367), ranging from about three-fifths the length of the humerus in some brachiosaurids to nearly four-fifths in some diplodocids (McINTOSH, 1990: 367). The expanded head of the ulna has a triangular cross section, being triradiate in proximal view. It has a concavity in front, to receive the head of the radius. This concavity faces anterolaterally, and is bounded by anterior and lateral projections; the former being the longer of the two (WILSON & SERENO, 1998: 26). The olecranon is absent or rudimentary, except in the Titanosauridae, where the ulna is well developed and massive (McINTOSH, 1990: 395).

The ulna bears marks and concavities for muscle attachment, but the nomenclature differs a bit from author to author. We have adopted herein the muscle nomenclature of BORSUK-BIALYNICKA (1977: figs. 8, 9 and 10), focusing only on the most important muscles (Fig. 9). The *triceps* (tric) is the muscle which attaches to the posterior wall of the olecranon and is responsible for the extension of the arm. The *interosseus* (ios) - a muscle which binds the ulna and the radius together, inserts in the ridge of the radial face of the ulna. The *flexor carpi ulnaris* (fcu) occupies the deep concavity on the medial wall of the head of the ulna. The *extensor carpi ulnaris* (ecu) and the *extensor digitorum communis* (edc) are two muscles which extend themselves along the shaft, until reaching a bulged area on the distalmost lateral portion of the ulna. They are housed into an ample depression located in the lateral side of the head of the ulna, behind the lateral expansion (BORSUK-BIALYNICKA, fig. 9, B and fig 10, B).

General observations:

Six ulnae compose the material under study (Tables 24 and 25, fig. 15). None of them has come from the "Serra da Galga" site. They may be separated in three size categories: small (MCT 1651-R), mid-size (MCT 1659-R, MCT 1676-R and MCT 1609-R), and large (MCT 1635 and MCT 1678-R) (Fig. 70 – C to E).

The ulna MCT 1609-R is of median size and is the only one from the "Rodovia" site (*fid.* Diógenes Campos).

Ulnae MCT 1651-R and MCT 1659-R were found at Site 1. MCT 1651-R is the smallest of all and must have belonged to a very young individual. MCT 1659-R is a mid-sized ulna.

Another ulna (MCT 1635-R) came probably from the same site, since it was collected in 1959, an year when Price was working at Site 1. In the quarry map of Price there are two large bones represented near a large pelvis (MCT 1536-R), which were collected in that year (CAMPOS & KELLNER, 1999: fig.3). MCT 1635-R may be one of them. It has undertaken some erosion, and is a little damaged in the extremities, but the rest of the shaft is in very good condition.

The ulnae MCT 1676-R and MCT 1678-R were recorded as from "Peirópolis surroundings". Although the available field information does not allow any confirmation, there is high possibility that these two bones have been also found in Site 1.

MCT 1676-R (left) has the same proportions and morphological features of MCT 1659-R (right), and they may be paired to each other. In fact, the morphologies of both bones are so alike (especially for the crenellated pattern of the distal surfaces) that it is possible that they have belonged to the same individual. Since MCT 1659-R has been unearthed from Site 1, MCT 1676-R must have been also unearthed there.

MCT 1678-R (right) is one of the largest ulnae, and shows exceptional state of preservation. It is almost the same size of MCT 1635-R (left) and shares the same morphology, making a pair with it. Since we considered that MCT 1635-R has been unearthed from Site 1, this would imply that MCT 1678-R would have been also found there. In fact, Price's quarry map shows a lot of large bones excavated in 1955, and some of them have an outline that corresponds to the shape of an ulna. This association should be regarded with caution, however, because, even though these two ulnae really belonged to the same individual, it is not quite certain if MCT 1635-R was really extracted from Site 1.

Morphology:

In natural position, the ulna should have the radial face directed towards the anterior extremity of the animal. If this real position is considered, then one should refer to it as radial view. In lateral and medial views, both lesser and greater expansions should

project themselves obliquely, the former anterolaterally, and the latter anteromedially. If depicted in one of these perspectives, these expansions have their proportions deformed, and thus look like shorter then they really are. Therefore, in the literature, the ulna is not depicted in the natural position, being rather figured a little medially twisted. This convention highlights the anatomic features of the bone. In this conventional pattern, Anterior view is considered as if the greater expansion faced direct towards the anterior extremity of the animal; and lateral view, thus, is considered as if the lesser expansion faced direct to the lateral side. The present study adopts this conventional pattern. Sometimes, however, it was necessary to depict the bones also in radial view. When this occurred, it was mentioned in the text or in the legend of the illustrations.

All ulnae display the general morphology found in sauropods in general (Figs. 30 and 31). It is a stout bone, with a straight shaft, which is expanded at both ends. The ulna looks like a three-faced piece, displaying a triangular profile in transverse section. The anterior face represents the radial surface, which is delimitated by two edges. The two remaining faces form the lateral and the medial sides of the ulna and meet together posteriorly, forming a third edge, which is opposed to the radial face. This edge is strongly arched backwards.

The head of the ulna is greatly expanded, and bears two expansions: a greater or anterior expansion (ant exp) and a lesser or lateral expansion (lat exp). They give the bone its typical triradiate proximal outline, and delimitate a strong, concave area for reception of the head of the radius - the radial fossa (rd fs). The radial fossa is anteriorly directed, but because the shaft of the ulna is a little twisted along its axis, the corresponding distal face for the articulation of the radius is a bit laterally directed. This conformation may provide a better accommodation for the radius, which is similarly twisted in Titanosaurids.

The anterior (or greater) expansion is broader than the lateral one, and about two times longer. Its tip is blunt. In lateral view, it grows just from the frontal border of the base of the olecranon and projects itself anteriorly at the same level as the lateral expansion, although with a lesser inclination, resting more horizontally. The lateral (or lesser) expansion is shorter and more pointed. It has a triangular outline and its superior border plunges down at an angle with the long axis of the bone, so that its tip ends at a point placed below the plane where the base of the olecranon rests. The upper surfaces of both anterior and lateral expansions bear small bumps and grooves. These could serve for muscle attachment, or could

be perhaps the remnants of cartilage. Their lower margins are smooth and gradually merge into the medial and lateral edges of the bone, respectively.

The ulna bears a rather developed spherical, blunt olecranon (ol) (Fig. 30; Fig. 31). It is conspicuous, projecting well above the shaft. It shows a smooth, spherical articular surface. In lateral view, the olecranon is rounded and bears no notch or groove (in contrast to *Alamosaurus* and the Saltasaurinae). The base of the olecranon is separated by the rest of the bone by a distinct, rugose line. This line could be a remnant of the joint capsule (BORSUK-BIALYNICKA. 1977: fig. 8a - j.c.).

In radial view, the lateral and medial borders of the ulna are arched and concave. The proximal portion is broader, and tapers gradually downwards until the superior third of the shaft. From that point on the shaft continues with a slender, persistently uniform breadth, expanding again at the very distal portion, although not as much as in the proximal one. The lateral and medial borders at the base of the distal end are not symmetrical, the medial being more expanded and prominent than the lateral. On the radial face, a longitudinal ridge (lng rdg) can be seen projecting at mid-length down the shaft until the distal border of the bone. This ridge is probably the area of insertion of the muscle *interosseus* (BORSUK-BIALYNICKA, 1977), and is also present in other Titanosaurid ulnae.

In lateral view, just behind the lateral expansion, the ulna bears an ample concavity, probably for muscles *extensor carpi ulnaris* and *extensor digitorum communis* (BORSUK-BIALYNICKA, 1977). Among the ulnae from Peirópolis, this concavity may be deep (in MCT 1609-R), shallow (in other ulnae), or almost flat (in the largest ulnae).

In medial view, the most striking feature of the ulna is a medial concavity (md conc) placed over the upper third of the bone, behind the anterior expansion (Fig. 30 – C). This concavity could house the muscle *flexor carpi ulnaris* (BORSUK-BIALYNICKA, 1977: fig. 8c – fcu).

The posterior border of the distal portion of the ulna bears a smooth bulge (Fig 30 – C - blg m.). This could be the insertion area for the attachment of a muscle, such as the *extensor digitorum communis* or the *extensor carpi ulnaris* (BORSUK-BIALYNICKA, 1977). This bulge may be the same previously noticed in a fragmentary ulna of *Laplatasaurus araukanicus* (HUENE, 1929).

The distal end is subtriangular and very rugose, unless in a limited smooth area, medially situated, where the bumps and rugosities are substituted by small holes (better

seen in MCT 1676-R). The margins show a series of crenellations and grooves. The grooves are more marked along the lateral margin.

Although all the six ulnae studied show the same general morphology, they differ in the shape of the distal articulating area for the radius. In this regard, two different morphotypes can be easily distinguished among the bones.

Morphotype 1

Material: MCT 1651-R, MCT 1659-R and MCT 1676-R.

Description: in morphotype 1, the longitudinal ridge (lng rdg) that runs down over the radial face delimitates a huge distal excavation (dst exc). This excavation begins at about the mid-line of the distal third of the shaft, and follows like a trench that, along its way down to the distal margin of the ulna, gets gradually wider and deeper (Fig. 31 – B). This feature is better seen in distal view. The presence of this excavation in the ulna makes its distal face looks like more reniform than subtriangular in outline (Fig. 31 – C).

MCT 1659-R (right) (Fig. 31; Fig. 67; Fig. 68 – A, B, C) and MCT 1676-R (left) (Fig. 68 – D, E, F): these two mid-sized ulnae are here considered to make a pair. The above description of morphotype 1 was based in these two bones.

MCT 1651-R (right) (Fig. 66 – D, E, F): the smallest of all and shows the same morphology of the previous two. The olecranon seems a little lesser developed and both extremities lack the profusion of bumps and grooves displayed by the others. This could be because MCT 1651-R belonged to a much younger animal.

Morphotype 2

Material: MCT 1609-R, MCT 1635-R and MCT 1678-R

Description: in morphotype 2 ulnae the longitudinal ridge (lng rdg) that is present in the middle of the shaft is more conspicuous and grows at about the middle of the long axis of the bone. It continues its way down to the distal portion but stops well before reaching the inferior border of the bone. Then the ridge is followed by a small higher protuberance. This

marks the apex of a triangular area (tr) that spreads itself over the distal articular facet for the radius (Fig. 30 – B). This triangular area is almost flat and placed at a shallower plane in relation to the radial face of the ulna. It is bordered laterally by a low ridge (which may be the continuity of the middle ridge) and medially by a small bump. The triangular area found in these large ulnae corresponds to the excavation displayed by the morphotype 1.

MCT 1678-R (right) (Fig. 30; Fig. 69, Fig. 70 - A) and MCT 1635-R (left) (Fig. 70 - B): these are the largest ulnae and show the same general morphology as the mid-sized ones. They are stronger and stouter, but this could be due to their belonging to a larger and heavier animal. The crenellating pattern shown in distal view is also present (although not exactly equal to MCT 1659-R and MCT 1676-R).

MCT 1609-R (right) (Fig. 66 – A, B, C): this ulna shows a slight difference on its lateral aspect, which distinguishes it from all the others: the depression which houses the muscles *extensor carpi ulnaris* (ecu) and *extensor digitorum communis* (edc) (BORSUK-BIALYNICKA, fig. 9, B and fig 10, B) is comparatively more deep than in ulnae MCT 1659, 1676 and 1651. In the largest ulnae, MCT 1635 and 1678, the same area is almost flat.

Comparisons within morphotypes:

The distal excavation displayed by morphotype 1 corresponds to the triangular area found in morphotype 2. Whether it is a true morphological difference, indicating different species, or just a variation related to size or age, is discussed below.

The smallest ulna (MCT 1651-R) and two mid-sized ulnae (MCT 1659-R and MCT 1676-R) belong to morphotype 1 category, while the two largest ulnae (MCT 1635-R and MCT 1678-R) belong to morphotype 2 category. This could suggest that morphotype 1 is related to small-sized or younger individuals, and, during growth, the ulnae should undergo morphological changes to become morphotype 2, which is found in larger, older animals.

Nevertheless, ulna MCT 1609-R is about the same size of ulnae MCT 1659-R and MCT 1676-R (morphotype 1), which suggests that the three bones belonged to animals of similar age. It displays, however, the typical trait of morphotype 2 - a triangular area on the distal radial articulating area. The presence of this trait in ulna MCT 1609-R suggests that

it is a true morphological distinction between the two morphotypes, and not the result of age development.

Comparisons with other taxa:

The ulnae of Peirópolis have been compared to the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Alamosaurus sanjuanensis*; *Antarctosaurus wichmannianus*; *Argyrosaurus superbus*; *Chubutisaurus insignis*; *Laplatasaurus araukanicus* (= *Titanosaurus araukanicus*); *Laplatasaurus sp.* (=*Antarctosaurus sp.*); *Saltasaurus loricatus*; *Opisthocoelicaudia skarzynskii*; *Titanosaurus australis* (=*Neuquensaurus australis*); *Titanosaurus colberti* and *Titanosaurus robustus* (=*Neuquensaurus robustus*).

As for the humerus, there are several titanosaurid species that may be distinguished from the Peirópolis ulnae by having a stockier bone.

There are right (MLP/CS 1095) and left (MLP/CS 1094) ulnae assigned to *Titanosaurus robustus* (HUENE, 1929). They differ from the Peirópolis material by several aspects. The proportion of the head of the ulna in relation to its total height, for instance. The shaft of the ulna of *T. robustus* seems to be less higher than two times the width of its head (HUENE, 1929: lam. 18, figs. 3 and 4). In the Peirópolis material, however, the height of all ulnae surpasses well the doubled dimension of the width of their respective heads. In MLP/CS 1094, the olecranon is not rounded, but divided in two pointed surfaces by a concavity (HUENE, 1929: lam. 18, fig. 4). This ulna seems also more bowed, the posterior margin describing a stronger curve than in the Peirópolis ulnae (HUENE, 1929, lam. 18, fig. 4c). In ulna MLP/CS 1095, the longitudinal ridge that runs over the radial face is conspicuous, and ends in a strong projection (HUENE, 1929: lam. 18, fig. 3a). The ulnae of *T. robustus* differ also from the Peirópolis material in distal view: the distal portion shows a suboval outline (HUENE, 1929: lam.18, fig. 4e), while it is reniform in morphotypes 1 and subtriangular in morphotype 2.

The left ulna of *Saltasaurus loricatus* (PVL 4017-74 - hypodigm) was previously considered similar to the ulna of *Titanosaurus australis*, but wider in the proximal area and with a probably higher olecranon process (BONAPARTE & POWELL, 1980: 22). It was latter considered more similar to the ulna of *T. robustus* (POWELL, 1992: 190).

The ulna of *Saltasaurus loricatus* is much more robust than the ulnae from Peirópolis, and, by the available drawings (POWELL, 1992: fig. 32), its shaft seems to be shorter than two times the width of its head (a trait that may be also present in *Titanosaurus robustus*). The olecranon is similarly well developed and backward projected. The distal articulation is rounded, with a reentrance on the internal face (POWELL, 1992: 191), a trait absent of all ulnae from Peirópolis. There is no available drawing of the distal face of the ulna, making it impossible to evaluate the presence, or not, of the distal excavation typical of morphotype 1.

The ulna of the holotype of *Opisthocoelicaudia skarzynskii* is stouter than the ulnae from Peirópolis (BORSUK-BIALYNICKA, 1977: fig. 8). The length of the shaft is only a little bit shorter than the doubled width of the head (BORSUK-BIALYNICKA, 1977: 28, and table 9), and this differentiates it from the Peirópolis material. It shows a very pronounced curved profile in mediolateral view (similar to *Titanosaurus robustus*). The ridge for the *interosseus* is present. The olecranon is rounded, and seems to be notched as in *Alamosaurus sanjuanensis* or *T. robustus* (BORSUK-BIALYNICKA, 1977: pl.9, fig. 1b). The area for the attachment of the *triceps* muscle is well marked, rugose, and directed backwards (BORSUK-BIALYNICKA, 1977: fig.8a, and pl.9, fig. 1b), a trait that may be also present in *Saltasaurus loricatus*.

The additional specimen of *Alamosaurus sanjuanensis* (USNM-15560) has a complete right forelimb, which was found articulated in the field (GILMORE, 1946). Its humerus is long in relation to the length of the radius and ulna (a character which, is difficult to be confirmed in the disarticulated material from Peirópolis). The ulna bears a stout, blunt olecranon process (GILMORE, 1946: 37). Posteriorly to the projection of the olecranon, and separated from it by a narrow notch, is a second, lesser projection (GILMORE, 1946: fig.9). This notch is not present in any of the ulnae of Peirópolis (although a similar condition – a concavity dividing the olecranon – may be present some Argentinean taxa, such as *Titanosaurus robustus*). The shaft of the ulna of *Alamosaurus* seems to have a abrupt constriction well marked below its middle (GILMORE, 1946: fig. 9), instead of gradually tapering downwards, as in the Peirópolis ulnae. The distal end of the ulna of *A. sanjuanensis* is reniform in outline (GILMORE, 1946: 37). In this aspect, it seems to match the Peirópolis morphotype 1 ulnae, which are also reniform in distal view. Unfortunately, GILMORE (1946) did not figure the ulna of *Alamosaurus* in that view, so the similarity remains uncertain until the material can be examined *in loco*.

The left ulna of *Titanosaurus colberti* (ISIR 335/60) differs in several aspects from the ulnae from Peirópolis (JAIN & BANDYOPADHYAY, 1977: fig. 22). The olecranon process is inconspicuous, the shaft is comparatively thicker, and both anterior and lateral processes seem more downward inclined than in the Brazilian bones. The distal end is subovate in outline (JAIN & BANDYOPADHYAY, 1997: 123), distinguishing it from the Peirópolis ulnae, whose distal ends are either reniform (morphotype 1) or "D" shaped (morphotype 2). The ulna of *T. colberti* bears a sharp ridge, which runs along the shaft of the ulna and merges into the distal end, and has medial and lateral concavities (JAIN & BANDYOPADHYAY, 1997: 123). These features, however, are normally present in other titanosaurid ulnae, including the Brazilian ones.

Some species are difficult to be compared with the Brazilian material.

The left ulna of *Chubutisaurus insignis* (holotype MACN 18222) is robust, and only the distal two thirds are preserved (McINTOSH, 1990: 384; SALGADO, 1993: 269), making comparisons difficult. The distal articular face for the radius is broad and more or less triangular in shape, and it is placed just below a longitudinal ridge that runs along the radial face. This features make this ulna more similar to morphotype 2.

The distal part of the left ulna of *Antarctosaurus wichmannianus* (holotype MACN 6904) has no excavation on its anterior distal articular face (HUENE, 1929: lam.30, fig.6), which differentiates it from morphotype 1 ulnae. The heads of some ulnae attributed to this species, housed at the Museo Argentino de Ciencias Naturales (Buenos Aires - Argentina), have a comparatively lower olecranon and longer anterior expansions (at least two times more than the lateral ones).

The ulna of *Argyrosaurus superbus* (holotype MLP.77-v-29-1) shows a very well developed olecranon, proportionally higher than in other titanosaurids. The radial ridge is also very prominent and is not restricted to the distal portion of the shaft, but extends itself well above the middle, almost reaching the radial fossa of the head of the ulna (personal observation). The additional specimen (PVL 4628) is difficult to compare by the available figures (e.g. BONAPARTE, 1996: fig. 43).

HUENE (1929) ascribed a right ulna to the hypodigm of *Laplatasaurus araukanicus* (MLP/Av. 2081). This bone , , lam.24, fig.1) may not belong to this species (BONAPARTE, 1996: 103). The ulna of *L. araukanicus* is very fragmented to be compared to the ulnae from Peirópolis. By the available drawings (HUENE, 1929: lam. 24, fig. 1c), it is possible to say that that the ulna of the Argentinean species lacks a distal excavation, resembling morphotype

2 ulnae. The posterior bulge present in the distal portion of the ulna (HUENE, 1929: lam. 24, fig. 1a) seems to be more pronounced in *L. araukanicus* than in the Brazilian bones.

An additional specimen – *Laplatasaurus sp.* is represented by an incomplete right ulna (PVL 3670-2), and a left one, badly preserved (POWELL, 1979). The available illustrations of the right ulna are not elucidative to make a good comparisons between that bone and the ulnae from Peirópolis. (POWELL, 1979: fig.3). Nevertheless, the radial face o *Laplatasaurus sp.* shows a longitudinal ridge (POWELL, 1979: 195), a trait that is also present in the Peirópolis material.

Of the titanosaurid species recorded so far, the most similar to the Peirópolis material are *Titanosaurus* (=*Neuquensaurus*) *australis* and *Aelosaurus rionegrinus*.

The hypodigm of *Titanosaurus australis* is represented by three ulnae (MLP/CS 1058, MLP/CS 1053, and MLP/CS 1306), which share some traits with the ulnae from Peirópolis. They are slender like, that is, the total length surpasses the doubled width of the heads (HUENE, 1929: lam. 11, figs. 1, 2, and 3). The olecranon is rounded and not divided by a notch. (differentiating both from *T. robustus*). The available drawings of the ulnae of *T. australis* in distal view (HUENE, 1929: lam. 11, figs.1e, and 3c), attest for the absence of a distal excavation in their radial faces, distinguishing them from morphotype 1.

As morphotype 2, however, *T. australis* displays a conspicuous longitudinal ridge running along its radial surface, but this seems more developed in the Argentinean species, specially in ulna MLP/CS 1053 (HUENE, 1929: lam. 11, fig. 2a).

The left and right ulnae of the holotype of *Aelosaurus rionegrinus* (MJG-R1) has been neither figured, nor described (POWELL, 1987b). Comparisons of the Peirópolis material with this species were possible based on some photos taken by one of us (A. Kellner) during a visit to the institution where it is housed (Museo J. Gerholdt, Ingeniero Jacobacci, Argentina). The ulna of *A. rionegrinus* looks like the Peirópolis ulnae, being slender. The olecranon is rounded, not notched. It lacks the anterior excavation at the distal end, differing thus from morphotype 1 ulnae.

There are two right ulnae referred to *Aelosaurus sp.* (SALGADO & CORIA, 1993a). The material comprises juvenile right ulna and radius (MPCA 27175) and a larger ulna (MPCA 27174). These ulnae share the same morphology with the holotype of *A. rionegrinus*, being less robust at both ends (SALGADO & CORIA, 1993a: 123). The following comparisons are based on the examination of MPCA 27175 (during a visit to the Museo

Provincial de Cipolletti - Rio Negro, Argentina), and the available figures and descriptions (SALGADO & CORIA, 1993a: fig. 5, and lam.1e).

The ulnae of *Aelosaurus sp.* resemble closely the ulnae of Peirópolis, but they bear no evidence of having a deep trench on the articular distal portion, differing from morphotype 1. The proximal ends are very alike, with a similar triradiated profile and, especially by the presence of a prominent, rounded, not notched olecranon. There is a longitudinal bony ridge running along the middle of the radial face (similar to morphotype 2).

Characters of the ulna described in previous Sauropod phylogenies:

Among the several previous sauropod phylogenetic studies using cladistic methodology, only the analyses carried out by UPCHURCH (1995) and by WILSON & SERENO (1998) dealt with characters concerning the ulna.

WILSON & SERENO (1998: 25) defined two characters for the sauropod ulna: olecranon reduced or absent (character n ° 4) and proximal end of ulna triradiate, with deep radial fossa (n° 5) ; each one with two states.

These authors argue that a prominent rounded olecranon, projecting itself above the proximal humeral articular surface of the ulna is the plesiomorphic state, present both prosauropods and basal theropods. In sauropods, in contrast, the olecranon is rudimentary or absent (the derived state). They recognize, however, that a well-developed olecranon is present only in titanosaurs, which is by them considered a reversal. UPCHURCH noted the presence of an olecranon among the members of his Titanosauroidea, a clade uniting *Opisthocoelicaudia* to Titanosauridae. He defined the character, however, as "anteromedial proximal process of the ulna bears a prominent concave area dorsally" (UPCHURCH, 1995: 379, fig. 14) . This concave area mentioned is the area over the anterior proximal expansion limited posteriorly by the anterior margin of the olecranon.

The second character of the ulna concerns to its proximal condyle shape (WILSON & SERENO, 1998, character n° 5). This condyle is subtriangular in theropods and prosauropods, with a shallow concavity for the radius. In Sauropoda, which display the derived state, the proximal condyle is triradiate and bears a deep radial fossa bounded by anterior and lateral projections (WILSON & SERENO, 1998: 26).

Both characters, unfortunately, are sinapomorphic for all Sauropoda, being useless in analysis within higher taxa, such as the Titanosauria.

RADIUS

In prosauropods and theropods, the radius is primitively straight, with a subcircular or oval distal end (WILSON & SERENO, 1998: 26). In sauropods, the shaft of the radius usually follows a gentle sigmoid pattern, going from weekly to strongly curved. The cross section of the radial shaft is nearly circular, but it gradually gets wider toward the distal end, becoming more rectangular and flattened anteroposteriorly (WILSON & SERENO, 1998: 26).

The radius in sauropods lays more or less in front of the ulna rather than to its side, not crossing it. The expanded proximal end bears a somewhat pointed expansion, directed medially (McINTOSH, 1990: 367). In titanosaurids, the radius is a stout bone, its both ends being abnormally expanded, and its distal margin is not perpendicular to the shaft, but rather downwardly inclined (McINTOSH, 1990: 367).

The radius is the point of insertion of several limb muscles (BORSUK-BIALYNICKA (1977: figs. 8, 9 and 10), but only the most important are treated here (Fig. 9). The *interosseus* (ios) is a muscle which inserts into a strong ridge that runs nearly the length of the posterior face of the radius, binding it together with the ulna. Both *biceps* (bi) and *brachialis inferior* (bri) are muscles that insert into the medial face of the radius, just below its proximal anteromedial prominence. The *pronator teres* (pt) inserts into a the medial face of the shaft and the *flexor carpi radialis* (fcr) inserts into the anteromedial face of the shaft, over the distal margin of it.

General observations:

11 radii compose the material under study (Tables 26 and 27; Fig. 16). They are distributed in three different sizes – large, mid-size and small (Fig. 83 – C to H). Some are robust and others are slender.

There are two radii from the "Galga" site: MCT 1595-R (left) and MCT 1598-R (right). Both are large bones, but still of different sizes, representing two individuals. MCT 1595-R is the largest radius of all. Both ends are eroded, but the stout shaft is in good state of preservation. This bone bears morphological features of its own, being different from all other radii. MCT 1598-R displays the general morphology found in other radii, being just more stout. Its extremities are a little damaged.

The provenance of radius MCT 1610-R (right) is recorded herein as "Rodovia?". This correlation has been made, because its year of collection (1967 or 1969) corresponds to the years of fieldwork in that site. If the assignment is correct, this is the only radius to have come from "Rodovia". It is a slender type, being little longer than MCT 1649-R (another slender type radius, discussed below).

There are three radii that have come from "Site 1": MCT 1648-R (left), MCT 1649-R (left) and MCT 1650-R (right). The three bones are of three different sizes (large, mid-size and small, respectively), indicating the presence of three different individuals. MCT 1648-R is the largest in the group, and it is destroyed at both ends by erosion. MCT 1649-R is a mid-sized bone. If compared with other radii of the same size and morphology (e.g. MCT 1638-R), it becomes evident that it belongs to a more slender type (similar to MCT 1610-R). MCT 1650-R is the smallest of all radii, and must have belonged to a young individual. Its assignment to a particular morphotype is uncertain.

There are three radii assigned to "Peirópolis surroundings": MCT 1636-R (right), MCT 1637-R (right) and MCT 1638-R (left).

MCT 1636-R is a stout bone, larger than the other two.

MCT 1637-R and MCT 1638-R are mid-sized, and morphologically similar, making a perfect pair. Although they are scored as "Peirópolis surroundings", it is probable that their site of provenance is actually "Site 1". These radii display the same proportions as ulnae MCT 1659-R and MCT 1676-R, articulating well with them. This association is the main reason to assign these radii to "Site 1" deposits.

Radius MCT 1673-R (right) is an isolated finding, not correlated to any of the three main collecting sites. It was found at 1 km north of Peirópolis (the date of collection is unknown), being very eroded and broken. Only the proximal and distal extremities were found in the DNPM collection. The middle of the shaft is probably lost. It was included in the present study because of the unique morphology of it anteromedial proximal projection, which is more developed than in other radii.

An extra radius, of unknown provenance (MCT 1707-R), was included in the present study due to its different morphology. This radius may come either from Peirópolis surroundings or from another place, maybe from the State of São Paulo.

Morphology:

The radii of Peirópolis bear some features in common. They are straight, a little curved backwards and elliptical in cross section, the longest diameter being the medial-lateral one. The shaft is twisted about 45° along the axis, so that the proximal half of the bone faces more laterally than anteriorly. The anterior face of the shaft is smooth and bears no traces. The posterior or radial face bears some features. The most evident are the *interosseus* ridge (ios) and the distal articular area (dst art) for reception of the distal end of the ulna (Fig. 32).

The *interosseus* ridge begins just below the level that delimitates the upper third of the bone, at the radial face. It runs diagonally downwards, heading to the lateral margin of the radius. In its way down, over the middle third of the bone, the ridge becomes progressively thicker, until it reaches the lower quarter. There it gradually merges into the lateral margin of the radius.

The distal articular area for the distal end of the ulna splays itself over the distal third of the radius. It is composed of a subtriangular depression (str) sided by a medial elevation (med el) (Fig. 32 – A, E). The subtriangular depression lays laterally, the upper vertex of it projecting itself beyond the level where the *interosseus* ridge disappears. The medial elevation is situated medially, and shows morphological variation in some radii. Some radii bear a microridge (mic) just at the base of the lateral border of this elevation (Fig. 32 – B).

Both ends of the radii are expanded, the distal one is just a little wider than the proximal (see Table 27). The proximal end bears a medial projection (med prj), which is, due to the twist of the long axis of the shaft, also a little anteriorly directed (Figs. 32; 33; 34). This projection is called anteromedial projection by some authors (e.g. HUENE, 1929; POWELL, 1992), and may be more or less developed. Below this projection, on the medial margin of the shaft, there is an elevation, which may have been the zone of insertion of the muscles *biceps* and *brachialis inferior* (m.bi) (BORSUK-BIALYNICKA, 1977: fig.8 c). This elevation is conspicuous in some radii, and almost absent in others.

In proximal view, the radius outline is suboval, more or less "D"-shaped, the bar corresponding to the flat surface which articulates with the radial fossa of the ulna. The proximal surface is flat and rugose. Its border is well marked by grooves.

The distal end bears a large distal lateral expansion (dst lat exp) upwardly curved (Figs. 32; 33). This expansion limits laterally the triangular shallow depression described above and is also the place where the *interosseus* ridge merges into the bone. Opposite to

this distal lateral expansion, the medial border of the radius is straight instead. In distal view the bone shows an elliptical outline, being anteroposteriorly flat. The ulnar border bears a concavity, which corresponds to the triangular shallow depression mentioned above (Fig. 32 - E). This concavity marks the division of the distal surface in two asymmetrical areas. The medial one is larger than the other, and also more rugose and rounded, and corresponds to the medial elevation. The lateral one is flatter, less rugose, and corresponds to the distal lateral expansion (Fig. 32 - E).

The *pronator teres* ridge (BORSUK-BIALYNICKA, 1977: fig. 8c) is not present in the Brazilian material, unless the medial ridges present in radii MCT 1595-R and MCT 1707-R represents its insertion in the medial border of their shafts.

The only synapomorphy described for the sauropod radius in the literature - radial distal condyle subrectangular with flat posterior margin for ulna (WILSON & SERENO, 1998: character n° 6) is present in all radii studied. All radii that are completely preserved show both ends extremely expanded, a trait which is considered a common feature in titanosaurids (McINTOSH, 1990: 367). The combination of these two traits gives support to the allocation of the Brazilian radii into the Sauropoda and into the Titanosauridae.

The radii under study herein show variation in respect to several traits mentioned above, such as: overall stoutness (slender or robust), development of the proximal medial projection and of the elevation for the *biceps* insertion, presence of ridges on the shaft other than the *interosseus* ridge, shape of the distal medial elevation. This variation led to the segregation of the radii in four different morphotypes.

Morphotype 1

Material: MCT 1598-R; MCT 1636-R; MCT 1637-R; MCT 1638-R and MCT 1648-R.

Description: the majority of the radii under study fall into morphotype 1 category. In fact, morphotypes 1 and 2 are very similar to each other, displaying the general morphology described above, differing in some details.

Morphotype 1 is characterized by having more robust shafts than morphotype 2. The medial projection is less developed. The elevation for the insertion of the *biceps* is absent or reduced to a gentle curve. The *interosseus* ridge is the only ridge running along the shaft. It begins in the upper third of the bone. The most different aspect of morphotype

1 in relation to morphotype 2 lays on the morphology of the medial elevation (med el) present on the distal articular face for the ulna. In morphotype 1, this elevation is more prominent and grows continuously until reaching the distal margin. This last character is better seen when the bones are observed in distal view (Fig. 33 – C; Fig. 81 – G, H) . The distal surface of the radius shows two condyles divided by a notch. This notch corresponds to the triangular excavated area of the ulnar distal face of the radius. In morphotype 1, the condyles are not symmetrically developed. The condyle that corresponds to the medial elevation (med el) is larger and circular in outline, whereas the condyle which corresponds to the distal lateral expansion (dst lat exp) is less developed and more anteroposteriorly flattened. In morphotype 2, both condyles are equally developed, and the condyle, which corresponds to the medial elevation, is more elliptical in outline.

The radii of morphotype 1 show some variations, which are discussed below.

MCT 1598-R (right) (Fig. 73): although the distal end of this bone is a little damaged, a more developed medial elevation is present in it, so it was assigned to morphotype 1.

MCT 1636-R (right) (Fig. 75): in medial view, the anterior border of the upper half of this bone is swollen and curved. This radius was assigned to morphotype 1 because of its stoutness, and the poor development of its proximal medial projection and the *biceps* insertion, which is marked by a gentle curve. MCT 1636-R is flattened in distal view, just like the radii of morphotype 2, suggesting that some differences between the two morphotypes could be less apparent in larger bones. Although it lacks a second ridge (as that present in MCT 1595-R), the surface of its shaft shows an incipient elevation, which marks a shift of planes just on the region where this second ridge should be.

MCT 1637-R (right) (Fig. 32; Fig. 76; Fig. 78 – B, D, F, H) and MCT 1638-R (left) (Fig. 33; Fig. 77; Fig. 78 – A, C, E, G; Figs. 79, 80, 81 – for comparisons): these are mid-sized radii that have been used as the basic description of morphotype 1. They are very well preserved, and make a perfect pair. If compared with other radii of the same size (e.g. the slender MCT 1649-R), these two bones show a more stout constitution. The *interosseus* ridge is strongly marked. It is long, beginning at the base of the upper third of the shaft. Both bones bear a small elevation, placed below the point were the *interosseus* ridge disappears, but medially dislocated. This elevation is better seen in MCT 1637-R and is also present, although weakly, in MCT 1649-R. It is not present, however, in other larger

radii. The medial projection emerges gradually from the medial margin of the shaft instead of abruptly, being for this reason less acute than in radii of morphotype 2. The *biceps* insertion is almost reduced to a scar, and is a little posteriorly displaced.

MCT 1648-R (left) (Fig. 79 – A, B, C, E): this bone is similar to MCT 1636-R, also bears an incipient elevation on the ulnar face and a swelling on the upper half of the anterior border of the bone. Both extremities were destroyed by erosion. It was assigned to morphotype 1 because of its robustness.

Morphotype 2

Material: MCT 1610-R; MCT 1649-R and MCT 1650-R.

Description: morphotype 2 is characterized by having a more slender shaft than morphotype 1. The medial projection is more detached than in morphotype 1, emerging abruptly from the medial margin of the shaft, being a bit more developed. The elevation for the insertion of the *biceps* (m.bi) is more conspicuous. There is no other ridge than the *interosseus* ridge running along the shaft. This ridge begins at about the middle of the shaft, and, although well marked, it is weaker than in morphotype 1 radii. An important trait to distinguish this morphotype from the previous one is the morphology of the medial elevation (med el). In morphotype 2, this elevation is more oval in shape, and it slopes down before reaching the distal margin of the radius. In distal view (Fig. 33 – C; Pl. R10 – G, H), the medial elevation (med el) displays almost the same diameter as the distal lateral expansion (dst lat exp), giving the bone a more flattened appearance (Fig. 33 - C).

As in morphotype 1, the radii assigned to morphotype 2 bear some variation.

MCT 1610-R (right) (Fig. 74): is slender, being little longer than MCT 1649-R, but morphologically similar. It is distinguished from other radii by some minor differences. The anterior face of the bone shows a shallow depression over the distal quarter (also present in MCT 1595-R). MCT 1610-R bears an elevation on the proximal surface, placed over the anterior corner of the anteromedial projection. Because the proximal surface shows some signs of erosion, we assume that this feature may be unnatural. This feature is not present in any other radius whose extremities are preserved.

MCT 1649 (left) (Fig. 33; Fig. 80 – B, D, F, H; Fig. 81 – B, D, F, H): if compared with MCT 1638-R (morphotype 1), which is almost the same size, this bone is slender. The distal anterior surface is flat. It is neither concave (as in MCT 1610-R and MCT 1595-R), nor convex (as in other radii).

MCT 1650-R (right) (Fig. 82): this bone is the smallest of all radii. Its most important feature is the development of the medial elevation for the insertion of the *biceps*, which is very conspicuous for a bone of this size. The head is inclined laterally, above the level of the *biceps* insertion.

Morphotype 3

Material: MCT 1595-R and MCT 1707-R

Description: morphotype 3 is characterized by the presence of an extra ridge (simple or doubled) running along the shaft of the radius. Nevertheless, the two radii included in this morphotype are very different from each other, and they may even represent morphotypes of their own. Unfortunately, they are so badly preserved, that a more complete morphological analysis is impossible so far. The two radii are briefly discussed below.

MCT 1595-R (left) (Fig. 34 – A, B; Fig. 72): is the largest radius of all, but both of its extremities are broken. This bone bears unique features, which distinguish it from all others. The most evident is the extremely development of the *interosseus* ridge. In this bone, this ridge is more pronounced than in any other radius, and extends itself well down the shaft. The ridge bears an enlargement (ios enl) along the last 5 centimeters, where it suddenly merges into the bone. This enlargement delimitates a deep area (2 cm wide, 1,5 cm deep), which forms an 8-centimeter trough between the ridge and the rounded condyle (Fig. 34 – A). At the present state of this study, we cannot assure that the final enlargement of the *interosseus* ridge is natural or abnormal. Opposite to the enlargement, on the lateral border of the rounded condyle, there is a small elevation. The second unique feature of this bone is the presence of a second ridge (sc rdg) on the shaft (Fig. 34 – A). This ridge lies centrally and obliquely on the ulnar face and parallels the *interosseus* ridge. It is, however, lower and shorter in both extremities, disappearing just when it enters the lower half of the shaft. The anterior surface of the bone is not smooth and uniform along the shaft, as in all

other radii, but it is crossed by an elevation which descends obliquely from the middle upper half of the bone towards its lateral border. The distal anterior surface of this bone is also marked by a shallow depression placed medially in relation to that elevation. The anterior face of the bone bears a shallow depression over the distal quarter.

MCT 1707-R (right) (Fig. 34 – D, E, F; Fig. 84): although also assigned to morphotype 3, this radius shows some features that differentiate is from the later. The shaft of MCT 1707-R is curved, differing from all other radii, whose shafts are straight. Nevertheless, it is a robust bone, with both ends extremely expanded, a common trait in titanosaurids dinosaurs (McINTOSH, 1990: 367). This bone shows a very concave proximal end, the distal end is very damaged, but it seems to be wider than the proximal one. The medial border of the shaft bears not only one, but two paralleled double ridges (dbl rdg) (Fig. 34 – E), and one of them, or both, could be perhaps the insertion area for the *pronator teres* muscle (BORSUK-BIALYNICKA, 1977: fig. 8 c). The medial projection is strong and upwardly directed. The *interosseus* ridge is also present, although in a weaker state than in other radii, and it begins well down the middle of the shaft. The presence of an enlargement at the end of its *interosseus* ridge, such as that present in MCT 1595-R, cannot be verified, due to the state of preservation of the distal portion. The elevation for the *biceps* muscle is present. The anterior distal surface is flat, not concave as in MCT 1595-R.

Morphotype 4

Material: MCT 1673-R

Description: morphotype 4 is similar to morphotype 2, unless by its proximal medial projection, which is extremely developed.

MCT 1673-R (right) (Fig. 34 – C; Fig. 83 – A, B): this radius is not related to any of the three main collecting sites. It was found at 1 km north of Peirópolis, being thus an isolated finding. The bone is broken in three parts, the middle third is lost, and the rest of it is very eroded. As in morphotype 2, the distal end of this radius is flattened. Its proximal medial projection, however, is strongly developed, being longer and thicker than in all other radii (Fig. 34 – C). Due to this exclusive morphology, we have assigned this radius to a category of its own - morphotype 4.

Comparisons within morphotypes:

As it was noted above, the radii may be divided in 4 morphotypes. Nevertheless, all bones are very similar to each other , with the exception of MCT 1595, from "Galga", MCT 1673-R and MCT 1707-R, which display a morphology of their own.

The radii of morphotype 1 and 2 are very alike, and can be distinguish from each other by minor differences of overall structure (Fig. 33 – A, B; Fig. 80; Fig. 81). The bones of morphotype 1 are stouter, bear a longer and stronger *interosseus* ridge, have a shorter anteromedial projection and bear a more prominent distal articular face for the ulna.

These differences, however, are easily identified among the radii when the bones in comparison are at about the same size, as is the case of all the mid-sized radii. Above or below this size, the distinction is less evident, and some bones may display morphological characters of both morphotypes discussed. The situation is complicated by the fact that even some radii bear some minor features, which appear not to be shared with others. The better examples come from MCT 1636-R and MCT 1650-R. The first is the second largest radius of all, and is well preserved. It shows the stout construction and the longer and stronger *interosseus* ridge typical of morphotype 1 bones. It has also a short anteromedial proximal projection. Nevertheless, in distal view, both condyles show the same degree of development, giving the distal surface the flattened elliptical typical of morphotype 2. It shares with MCT 1637-R and MCT 1638-R the presence of a microridge, and, with MCT 1650-R, the inclination of the head . This inclination is also present in other mid-sized radii, although not so evident. MCT 1636-R shares with other large radii the bulge of the upper anterior surface, and, with MCT 1648-R, the presence of a second, incipient elevation on the ulnar face of the shaft.

MCT 1650-R, for its turn, is the smallest of all radii, and bears yet the most prominent insertion for the *biceps* among all other bones. This bone shows poor development of the ulnar condyle, so it is difficult to assign it either to morphotype 1 or 2. The longer anteromedial proximal projection and the overall slender profile of its shaft are decisive for its placement in morphotype 2 category.

Three morphological characters which are present exclusively in some radii are a small elevation (el) near the root of the *interosseus* ridge (exclusive of MCT 1637-R and MCT 1638-R; very incipient in MCT 1649-R) ; presence of a second ridge at the ulnar face of

the radius, paralleling that of the *interosseus* (this feature appears only in MCT 1595-R) and presence of a shallow depression over the distal anterior face of the bone (this is shared both by MCT 1610-R and MCT 1595-R).

The diversity of morphological characters widespread among the material has made its subdivision in morphotypes not an easy task. These characters may perhaps just mean that the radii suffer a kind of morphological rebuilt during normal ontogeny. They may just indicate differences between male and female individuals. The strange morphology of MCT 1595-R may be just the extremely development of muscular insertions in animals of grater size. Unfortunately, the bone is destroyed in both extremities, so other features, such the development of the anteromedial proximal projection cannot be evaluated. The presence of incipient second ridges over the ulnar faces of MCT 1648-R and MCT 1636-R, bones which are just slightly smaller than MCT 1595-R, may be the proof of an intermediary stage of development of this ridge, which should be absent in smaller forms, appearing later in development of the animal, progressively becoming more pronounced while the animal was getting older.

Despite of the troubles above mentioned, the division of the material between morphotype 1 and 2 categories seems to work well, but should be envisioned with caution, since they alone may not serve for the designation of more than one different species.

Comparisons with other taxa:

The Peirópolis radii have been compared with the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Alamosaurus* ***sanjuanensis***; ***Argyrosaurus*** *superbus*; *Chubutisaurus insignis*; *Laplatasaurus araukanicus* (=*Titanosaurus araukanicus*); *Laplatasaurus sp.* (=*Antarctosaurus sp.*); ***Opisthocoelicaudia skarzynskii***; *Saltasaurus loricatus*; *Titanosaurus australis* (=*Neuquensaurus* ***australis***); *Titanosaurus robustus* (=*Neuquensaurus robustus*).

The radius of the holotype of *Opisthocoelicaudia skarzynskii* is different from all Brazilian radii. The bone is pillar like, bilaterally symmetrical, differing from the sigmoid profile generally found in titanosaurids (BORSUK-BIALYNICKA, 1977: fig. 8). The bone has both ends extremely transversely expanded – the proximal and the distal breadth are about 50% and 40% of the bone length, respectively, whereas the breadth of the most constricted

region of the shaft makes only 20% of the total length (BORSUK-BIALYNICKA, 1977: 27). This rate is never found among Peirópolis bones, whose proximal and distal breadth range between 25% to 30% of their total lengths. The *interosseus* ridge is present. A second crest which extends from about the proximal one third of the postero-medial border of the bone distally and slightly laterally, is present, and is considered to be the insertion for the muscle *pronator teres* (BORSUK-BIALYNICKA, 1977: 27). This crest is not present in the Peirópolis material, with the exception of MCT 1707-R, whose medial double ridges could perhaps represent such a structure.

There are several titanosaurid species whose radii are known, but these are either incomplete, or just briefly described in the literature. Fruitful comparisons between those species and the Brazilian radii require further examination of those materials *in loco*. The following comparisons are therefore tentative.

The right radius of *Alamosaurus sanjuanensis* (additional specimen USNM-15560) is figured in frontal view (GILMORE, 1946: fig. 9a). It an extremely expanded distal end, more than in any of the Peirópolis radii. The broken distal ends of MCT 1595-R and MCT 1707-R make it impossible to compare them with *A. sanjuanensis* in this respect. There is no figure of its ulnar face, therefore, any further comparison between the Brazilian and the North American material is impossible.

The holotype of *Argyrosaurus superbus* (MLP 77-v-29-1) is a gigantic specimen, characterized by robust limb bones (BONAPARTE, 1996: 109). HUENE (1929: 78) described briefly the specimen, emphasizing its stoutness, but gave no much details of its morphology. During a visit to the La Plata Museum (Argentina), we have examined the bone. It's very damaged, but, although large, the shaft is comparatively slender in relation to the largest radii of Peirópolis (e.g. MCT 1595-R and MCT 1636-R). Additional material referred to *Argyrosaurus* (PVL 4628) is not figured in detail (BONAPARTE, 1996: fig. 43), but the drawing shows a radius of normal shape.

The left radius of the holotype of *Chubutisaurus insignis* (MACN 18222) is only briefly described as a robust element, which distal end is more greatly expanded than the proximal one (McINTOSH, 1990: fig. 16.12 e). This accords with the normal morphology of the Peirópolis radii, which are also more expanded distally than proximally (Table 27). Nevertheless, the degree of expansion of the distal end of *C. insignis* is higher than in any of the Peirópolis material (personal observation). A redescription of *C. insignis* (SALGADO, 1993) gives no minute details of its morphology. The radius of

Chubutisaurus insignis seems to be less twisted than in other titanosaurians, including the Peirópolis specimens. The head is oval in proximal view. The mounting of the bones in the MACN exhibition makes is difficult to visualize other features of both radial and ulnar articular faces.

The bones of *Saltasaurus loricatus* are known to have belonged to individuals of different sizes and ages (POWELL, 1992: 191). The distal border of the right radius (hypodigm PVL.4017-76) is more inclined than in any of the Brazilian radii (POWELL, 1992: fig. 34). This taxon bears a second longitudinal ridge (POWELL, 1992: fig. 34), which may be similar to that present in radius MCT 1595-R (morphotype 3). Unfortunately, the distal end of MCT 1595 is damaged, so, it is not possible to say if its distal border is equally inclined as in the Argentinean taxon. The radius of the juvenile individual of *Saltasaurus loricatus* (PVL 4017-78) shows a strong sigmoid shaft, with all the distal portion well displaced laterally (POWELL, 1992: fig. 33). This character is not found in any of the Brazilian radii, even MCT 1650-R, which is also considered to belong to a juvenile.

Some titanosaurid taxa bear some features in common with the radii from Peirópolis. Some species (e.g. *Titanosaurus robustus* and *Titanosaurus australis*) may share some traits with more than one morphotype. Other species may be more similar to one morphotype alone.

Titanosaurus robustus has only one left radius available (MLP CS/1171). The available figures of this bone are not elusive at all (HUENE, 1929: lam. 18, fig. 5). Nevertheless, the radius of *T. robustus* seems to share some traits with morphotypes 1, 2, and 4. With morphotype 1, it shares the more robust constitution and the prominent distal articulating area for the ulna. It also bears a strong and well marked *interosseus* ridge. As in morphotype 2, it has a well marked elevation for insertion of the *biceps*. Its medial projection, however, is much more developed (HUENE, 1929: lam 18, fig. 5a), arising abruptly from the medial margin of the shaft, resembling, in this respect, MCT 1673-R (morphotype 4).

There are several radii attributed to *Titanosaurus australis* (hypodigms MLP CS/1169, 1172, 1174, 1175, and 1176), and they display considerable morphological variation (HUENE, 1929: 39). The medial projection of *T. australis* detaches itself gradually from the shaft, instead of abruptly (HUENE, 1929: lam. 11, figs. 4 to 8), resembling the condition seen in morphotype 2. In fact, MLP CS/1169 (HUENE, 1929: lam 11, fig. 8) is very alike morphotype 2, since it bears a prominent *biceps* elevation and seems to have a less developed *interosseus* ridge. In distal view, this radius is flatter than the others, and its distal articular condyle is not much developed. Another radius - MLP CS/1175 (HUENE, 1929: lam. 11, fig.

1) shows a more protuberant distal articular condyle in distal view, as well as a stronger *interosseus* ridge, resembling, thus, morphotype 1.

Notwithstanding those similarities, the ulnar face of the radii of *T. australis* has two longitudinal oblique ridges running from the proximal end of the articular face down to the lateral expansion of the articular distal end. The ridge, which is placed below the medial projection, is longer and stronger than the other, which is weak (HUENE, 1929: 39). The two ridges are not clearly visible in the available figures (HUNE, 1929: lam 11), making comparisons uncertain. The presence of this trait should distinguish *T. australis* from both morphotypes 1 and 2, approaching it to morphotype 3, specially MCT 1707-R, which also has two parallel medial ridges on its ulnar face. The present considerations must be regarded with caution, however, since the hypodigm of *T. australis* may represent more than a single species (BONAPARTE, 1996: 105).

The radii of *Aelosaurus rionegrinus* (holotype MJG-R1) are not figured in the original description (POWELL, 1987b). The following comparisons were based on some photos of the holotype, taken by one of (A.W. Kellner), during a visit to the institution where it is housed (Museo J. Gerholdt, Ingeniero Jacobacci, Argentina). The radius of *Aelosaurus rionegrinus* shares some traits with morphotype 2 radii from Peirópolis. The shaft is slender, the *interosseus* ridge is short and not so strong, and the medial elevation placed on the ulnar distal articular area has exactly the same shape as in the Brazilian material. In anterior view, the radius of *A. rionegrinus* shows an elevation over the superior border of the medial projection, similar to that found *in* MCT 1610, suggesting that this trait may be natural, and not an artifact of preservation.

There is an additional right radius (MPCA-27175) referred to *Aelosaurus sp.* (SALGADO & CORIA, 1993a, fig. 6). *In* overall shape, it is slender, also resembling morphotype 2 radii. Although not figured in distal view, it also shows an ovoid protuberance on its distal articular surface. Its medial projection is similarly developed, and the *interosseus* ridge is less developed than in morphotype 1. A remarkable difference, however, lies on the presence of two bony ridges over the ulnar face (SALGADO & CORIA, 1993a: fig. 6). These bony ridges are neither present in morphotype 1, nor in morphotype 2. They are also different from the ridge present in the ulnar face of MCT 1595-R (morphotype 3), which is longer, and from the double ridges of MCT 1707-R, which are placed along the medial border of its shaft.

The species *Laplatasaurus araukanicus* was described based on some associated material from Rancho Ávila (Argentina), which included a right radius (MLP Av. 2072), and also in an unrecorded left radius (from site of Dr. Wichmann's findings), of similar morphology (HUENE, 1929).

The radius of *Laplatasaurus araukanicus* is easily distinguished from all others by several traits (HUENE, 1929: lam. 24, figs. 2 and 3). The articular proximal surface of the head is not flat, as in normal radii, but very concave, the borders of it projecting upwards, surpassing the longitudinal extension of the bone (HUENE, 1929: 58). The distal end is asymmetrically enlarged, and the shaft is S-curved. These traits are not present in any of the Peirópolis radii, and may be perhaps unique to *Laplatasaurus*.

The radius from Wichmann's material (HUENE, 1929: lam. 24, fig. 3), however, is very similar to the Brazilian radius MCT 1707-R (of unknown provenance), which also has a proximal concave surface, a upwardly projected medial border, a S-curved shaft and two longitudinal oblique ridges. This last trait was noticed in the Argentinean specimen only in transverse section (HUENE, 1929:58). The presence of an asymmetric enlargement of the distal end cannot be properly evaluated in MCT 1707-R, for its distal extremity is severe damaged. The presence of so many similarities between *Laplatasaurus araukanicus* and MCT 1707-R makes it interesting to examine the species at the La Plata Museum.

The additional specimen referred to *Laplatasaurus sp.* (POWELL, 1979) is represented by an incomplete right radius (PVL 3670-3). Although it is too poorly preserved, it can be distinguished from all Peirópolis radii by the great development of its posterior distal extremity, which gradually expands itself from the beginning of the inferior third of the bone (POWELL, 1979: 196). This trait, however, cannot be evaluated in MCT 1707-R, whose distal end is broken. The given figures (POWELL, 1979: fig. 3) do not allow further considerations.

Characters of the radius described in previous Sauropod phylogenies:

Among the several previous sauropod phylogenetic studies using cladistic methodology, only the analyses carried out by WILSON & SERENO (1998) dealt with characters concerning the radius.

These authors described only one character of the radius (character nº6): distal condyle of radius subrectangular, with flat posterior margin for ulna. In prosauropods and

theropods, which bear the plesiomorphic state, the radius has a subcircular of oval distal end. In sauropods, the distal end of the radius is flattened anteroposteriorly (WILSON & SERENO, 1998: 26). As for the ulna this character is sinapomorphic for all Sauropoda, and the Brazilian material, which also bear flattened distal ends, is no exception.

PELVIC GIRDLE AND POSTERIOR LIMB

PUBIS

The pubis is one of the three paired bones that – together with the ilium and ischium – compose the pelvic girdle. Each of the three bones has processes contacting the other two, forming an articular socket for the reception of the head of the femur - the acetabulum. The open acetabulum is more or less diagnostic of the pelvis of the Dinosauria (RASSKIN-GUTMAN, 1997: 536). In lateral view, the pelvic girdle displays a triradiate outline. The ilium extends dorsally and the pubis and the ischium are positioned ventrally, with the pubis placed anteriorly, and the ischium posteriorly. Plesiomorphically, the pubic shaft points forward in the Saurischia (propubic condition) (RASSKIN-GUTMAN, 1997: 536).

In the Sauropoda, the pubis is generally larger and more robust than the ischium. Primitively, the blade forms an apron and the transverse diameter of the shaft greatly exceeds the sagittal one (McINTOSH, 1990: 369). In *Vulcanodon* the pubes resemble those of the prosauropods, with their shafts twisted to form a transverse apron. In *Barapasaurus* the pubis has a slender shaft and a relatively long symphysis, resulting in a pelvic cavity smaller than in later sauropods, but greater than in prosauropods (McINTOSH, 1990: 377).

In derived sauropods, the shaft is also apronlike, with a much expanded distal end. The pubis bears an opening - the pubic foramen. This foramen appears closed in all adult forms (McINTOSH, 1990: 369). Among the different families, the pubis retains a somewhat basic pattern, varying mainly in stoutness. In the Camarasauridae (represented by *Camarasaurus*) the pubis is relatively robust (McINTOSH, 1990: 386). In the Brachiosauridae (represented by *Brachiosaurus*) the pubis is massive and lacks the ambiens process on the proximal end (McINTOSH, 1990: 382). In the Diplodocidae Diplodocinae, the pubis has a relatively long, slender shaft and has a developed process on

the cranial margin for the attachment of the *ambiens* muscle. This process is prominent and hooklike in *Diplodocus* (McINTOSH, 1990:389); and not so strongly developed in *Barosaurus* (McINTOSH, 1990:390), and much less developed in *Apatosaurus* than in the two previous taxa (McINTOSH, 1990:391). In the Diplodocidae Dicraesaurinae (represented by *Dicraeosaurus*), the shaft of the pubis is also long and slender, with a prominent hooklike *ambiens* process (McINTOSH, 1990: 393). In the Titanosauridae, (represented by *Saltasaurus*) the shaft of the pubis is slender, and the distal end is expanded (McINTOSH, 1990: 395).

The pubis is an important site of attachment of several muscles of the hind limb (BORSUK-BIALYNICKA, 1977: fig. 12 and 17), but only the two most important are considered herein: the *ambiens* (amb) and the *puboischiofemoralis externus* (pife) (Fig. 10). The *ambiens* inserts itself on the anterior margin of the iliac peduncle of the pubis, extending itself downwards, until reaching the cnemial crest of the tibia. The *puboischiofemoralis externus* fills the latero-posterior concave surface of the pubis, extending itself posteriorly both to the ischium and to the medial margin of the femur.

General observations:

Eight pubes compose the material under study (Tables 28 and 29, Fig. 17). They show different morphologies, sizes, and degrees of preservation (Fig. 93 - B to E).

There are three pubes from the "Serra da Galga" deposits: MCT 1591-R, MCT 1592-R and MCT 1711-R.

MCT 1591-R (right) and MCT 1592-R (left): are the same sizes and display a morphology of their own. Therefore, they are considered as being the paired bones of a single individual. MCT 1591-R is in good state of preservation, being fairly complete – it lacks the portions corresponding to the ischial pedicle and has an eroded distal end. MCT 1592-R is the best preserved of all pubes from Peirópolis, maintaining complete ischial and iliac peduncles. MCT 1711-R (right) is the largest of all pubes from Peirópolis. It is broken in the middle, but the two parts fit well together, maintaining its original dimensions. The proximal part shows severe marks of erosion, but the rest bone is in good state of preservation.

MCT 1611-R (left) is the only pubis that has been assigned to the "Rodovia" site. Unfortunately, it is reduced to a small fragment of the distal shaft, not useful to morphological studies.

The remaining four pubes have unknown origin, so they have been all scored as "Peirópolis surroundings".

Two of them (MCT 1641-R – left, and MCT 1675-R – right) are the same size and display the same morphological patterns. They form a pair, and may have belonged to a single individual. Both bones are in good state of preservation, unless for some broken extension of the ischial pedicle and the pubic symphysis. MCT 1641-R is the best preserved of the two. It is possible that they have been unearthed from "Site 1", since this site has also yielded two pelves (CAMPOS & KELLNER, 1999). The lack of field data, however, makes this correlation uncertain.

MCT 1640-R (right) is well preserved, particularly for the ischial pedicle. The pubic symphysis is irregularly broken. It is the same size of the previous two, but differs morphologically from them. Nevertheless, it is possible that this pubis has been found also in "Site 1".

The last pubis, MCT 1677-R (left), is the second largest pubis in the material and, although incomplete, it is excellently preserved. The pubic symphysis is irregularly damaged, and the distal end is broken and lost. The association of this pubis with the pelves of "Site 1" is impossible, because the bone is too large. Therefore, this pubis may have been an isolated finding.

Morphology:

The proper orientation of the pubis in the sauropod pelvis lays on a line, which extends from the pubic pedicle of the ilium forwards and downwards, at about 45° from horizontal plane, at the same time it gradually converges from the lateral side to the middle of the skeleton. The bone, so, assumes a rather oblique orientation, not suitable for morphological descriptions. In the following analysis, we have assumed a completely vertical orientation for the bone, coincident with its longest axis, so that both lateral and medial views face the whole lateral and medial surfaces of the bone, respectively. The proximal and distal surfaces lay over horizontal planes parallel to each other and to the

ground. The anterior view faces the iliac pedicle and the pubic apron, and the posterior view envisages the articular surface for the ischium and the pubic symphysis.

The pubes from Peirópolis display the normal general morphology of the sauropod pubis (Figs. 35 and 36). The shaft is long and twisted, with both ends expanded. The proximal end is exaggeratedly expanded, and the distal one is moderately expanded, so that the bone assumes a rather "T" shape in lateral view, with the posterior bar of the "T" pendant. Both anterior and posterior margins are concave.

In lateral view, the expanded proximal half is divided into anterior and posterior portions, delimitated by the pubic foramen (pu fo). The anterior portion corresponds to the iliac pedicle (il ped), the posterior corresponds to the ischial pedicle (is ped) (Figs. 35 and 36).

The iliac pedicle has a columnar shape; its anterior margin is continuous with the anterior margin of the bone and projects itself forward. The superior margin is straight and horizontally set. Its posterior portion slopes down a little, just in the region that contributes to the acetabulum. The column is delimitated posteriorly by the pubic foramen. The pubic foramen is oval; its longest axis is set vertically. It is opened in most pubes, but appears closed in the largest pubes (MCT 1677-R and MCT 1711-R). This is a common trait in adult forms (McINTOSH, 1990: 369).

The ischial pedicle begins just behind the pubic foramen, and projects itself backwards and downwards, in an oblique line, set at about 30° from the horizontal upper margin of the iliac pedicle. This oblique line extends through the upper third of the pubis, where it than turns to merge into the pubic symphysis (pu sym) (Fig. 35 – A, B). Contrary to the columnar nature of the iliac pedicle, the ischial pedicle is a laminar structure, and its articular surface is curved, so that, if viewed posteriorly, the lateral margin is convex and the medial one is concave (Fig. 35 – B; Fig. 36 - D).

The lower two thirds of the pubic bone are dominated by the pubic apron (pu apr) (Fig. 35 – A). This is long structure, which corresponds to the vertical bar of a "T". Its shaft is straight, and its long axis is set at a right angle to the upper margin of the iliac pedicle. The pubic apron is twisted, achieving the typical canted posteromedially morphology present in all Sauropoda (WILSON & SERENO, 1998: character n° 46). The distal end of the pubic apron is also moderately expanded anteroposteriorly. In medial view, the most important traits are the greater diameter displayed by the pubic foramen, and the uniform flat smooth surface of the pubic apron.

In anterior view, the pubis assumes a blade like profile, being extremely thin in relation to its total length. The iliac pedicle may appear either mediolaterally compressed (in MCT 1591-R and MCT 1592-R) or a little expanded in relation to the apron width (all other pubes). The scar for the attachment of the muscle *ambiens* (m. amb) is clearly seen on the anterior margin of the iliac pedicle (Fig. 35 – A; Fig. 36 – C, E).

In posterior view, the bone reveals the laminar nature of both ischial and pubic articular surfaces. The ischial articular surface, which dominates the upper third of the bone, bears a strong, almost "U" shaped curvature, where the convexity points to the lateral side, and the concavity to the medial. Reaching the middle third of the bone, the laminar articular surface, now known as the pubic symphysis, continues in a straight line down to the distal end of the pubic apron. The ischial articular surface is rugose. The pubic symphyses are all too damaged and their articular surfaces are incomplete.

In proximal view, the articular surfaces of both iliac and ischial pedicles are clearly visible. These are rugose, and covered by grooves. In all pubes the iliac pedicle is longer than wide, but its outline varies from an elliptical (MCT 1592-R, MCT 1641-R) to a triangular shape (MCT 1640-R, MCT 1677-R) (Fig. 35 – B, D; Fig. 36 – D). The ischial pedicle is longer and thinner, and displays its normal laminar curved shape, with a medially set concavity. The acetabular portion (pub act) of the pubis is not well discernible among the elliptical iliac pedicles, being distinct only in those pubes with triangular pedicles (Fig. 35 – B).

Besides all these common traits, the pubes of Peirópolis also have individual morphological variations, which have allowed their segregation into three well distinct morphotypes.

Morphotype 1

Material: MCT 1641-R, MCT 1675-R and MCT 1711-R

Description: the pubes of morphotype 1 are robust and mediolaterally expanded. The anterior margin of the pubis follows a concave curve, from the anterior upper corner of the iliac pedicle down to the anterior margin of the distal end. This curvature is continuous, lacking the typical slope present in morphotype 2 and the rupture of morphotype 3. The insertion point for the *ambiens* is well marked on it by a rugose area, which is set at the same level

(differing from the other morphotypes). Because this curvature is so strong, the iliac pedicle is a bit forward projected, as well as the distal end of the pubic apron. The shaft displays an elevated lateral ridge (lat rdg), similar to a ripple, which runs over the lateral surface of the pubic apron (Fig. 35 – C; Fig. 36 – C, E). The ridge covers the two upper thirds of the pubic apron, dividing it in two distinct anterior and posterior regions. The anterior region is wide, flattened, and faces anteriorly. The posterior region is deeply excavated, forming a perpendicular angle in relation to the laminar process of the pubic symphysis. The ridge disappears at the beginning of the lower third of the pubic apron. The posterior excavated region must have housed the muscle *puboischiofemoralis externus* (pife) (BORSUK-BIALYNICKA, 1977: fig. 12 and 17). In anterior view, the pubic shaft displays straight lateral and medial margins. It is wider than in morphotype 2 due to the presence of the lateral ridge, which has a flattened anterior surface. The cross section of the shaft in morphotype 1 results in a triangular outline, with the base set anteriorly, and the vertex pointing backwards. This is distinct from the elliptical cross section of morphotype 2.

MCT 1641-R (left) (Fig. 35 – C, D; Fig. 89; Fig. 90 - B) and MCT 1675-R (right) (Fig. 90 – A, C): these pubes make a pair, and they have been the base of the morphotype 1 description. The iliac pedicle is anteriorly projected. The upper margin is convex, and the rugose acetabular portion is distinct, a little beveled laterally. The pubic foramen is set just behind the iliac pedicle. It is rather elliptical in outline, and the long axis stays almost vertical. In proximal view, the iliac pedicle is transversely compressed, being longer than wide, and more or less elliptical, having a pointed anterior margin. This is the same shape found in morphotype 2, but looks different in the other pubis assigned to morphotype 1 (MCT 1711-R – see below). Their ischial pedicles are damaged (just the portion set immediately behind the pubic foramen is preserved), hindering the evaluation of character nº 95 of WILSON & SERENO (1998).

MCT 1711-R (right) (Fig. 92): this is the largest of all pubes from Peirópolis. The presence of a lateral ridge on the pubic apron identifies this bone as belonging to the Morphotype 1 category. Furthermore, the anterior margin of the iliac pedicle is continuous with the concave anterior margin of the pubic shaft, and anteriorly projected, separating it from the morphotype 3 category. In distal view, the iliac pedicle is much more mediolaterally expanded, and rather rectangular in shape, suggesting that MCT 1711-R is an oversized version of MCT 1641-R and MCT 1675-R. The pubic foramen is closed, but

the suture line is still clearly visible. It is placed not far from the proximal margin of the bone. The distal anterior margin of the pubic apron is well forward projected. The most interesting feature of MCT 1711-R (which seems to be unique to this bone – at least among titanosaurids) is the shape of the anterior margin of the iliac pedicle. In other pubes, it is anteriorly projected, and somewhat pointed. In MCT 1711-R, however, this pointed extremity curves itself down. This trait is similar to the hook-like process displayed by some diplodocoid sauropods, such as *Diplodocus* and *Dicraeosaurus* (McINTOSH, 1990: 370, fig. 16.14). Some morphological traits, which were highlighted in the other large pubis from Peirópolis (MCT 1677-R), are not so distinct in this large pubis. The lateral ridge and the *ambiens* scar, for instance, are proportionally less developed than it would be expected in a bone of this size.

Morphotype 2

Material: MCT 1591-R and MCT 1592-R

Description: the pubes of morphotype 2 are distinguished by having the pubic apron slender than morphotype 1. Its lateral surface is slightly convex over the middle third, lacking the strong ridge seen in morphotypes 1 and 3. Its cross-section is oval, not triangular. In lateral view, the shaft is long and straight, the upper two thirds of it are dominated by a anteroposterior expansion which contains both iliac and ischial pedicles. The iliac pedicle projects itself well anteriorly; its upper margin is horizontally straight. Another important trait to differentiate morphotype 2 from 1 is the presence of a slope on the anterior margin of the bone (Fig. 35 – A – sl). This slope is placed at the base of the iliac pedicle, and is marked by a rugose prominence. The position of this prominence is coincident with the insertion area for the muscle *ambiens* (BORSUK-BIALYNICKA, 1977: fig. 12 and 17).

In proximal view, the iliac pedicle is long and narrow, compressed mediolaterally, being similar to morphotype 1 in this respect. The lateral margin is slightly concave; the anterior one is pointed. The division between the articular iliac surface and the acetabular portion of the pubis is not much distinct.

MCT 1591-R (right) (Fig. 87) and MCT 1592-R (left) (Fig. 35 – A, B; Fig. 86): the prominence that marks the slope typical of morphotype 2 is stronger in MCT 1591-R than in

MCT 1592-R. The pubic foramen is almost closed in both bones. It has a elliptical, rather eye-shaped outline, with the edge facing downwards, and is almost vertically set. Its diameter is greater in the medial side of the bone. Just behind the foramen is set the ischial pedicle. MCT 1592-R is the only pubes to have it complete. So it is the only bone where the character n° 95 of WILSON & SERENO (1998) may be evaluated. According to those authors, in eusauropods, the ischium and pubis meet below the acetabulum along a dorsoventral contact, which represents approximately one-third of the total length of the pubis. In *Camarasaurus* and Titanosauriformes (which display the derived state), the this contact is relatively deeper, constituting 45% to 50% the total length of the pubis (WILSON & SERENO, 1998: 51). In MCT 1592-R, the length of the ischial articular surface makes only 35% of total length of the pubis. This is just a bit more than one third (33,3%), and suggests that either MCT 1592-R belonged to a non-*Camarasaurus* – Titanosauriformes clade species, or that it was a titanosaurid which had retained primitive characters in the pubis.

Judging for its overall outline shape, MCT 1652-R was the titanosaurid pubis figured by McINTOSH (1990: 370, fig. 16.14 n), based on a photography sent by L.I.Price.

Morphotype 3

Material: MCT 1640-R and MCT 1677-R

Description: the pubes of morphotype 3 are similar to those of morphotype 1 in possessing a longitudinal elevated lateral ridge (lat rdg) (Fig. 36 – C and E) over the lateral surface of the pubic apron. They differ from morphotype 1, however, in the shape and development of the iliac pedicle. The iliac pedicle of morphotype 3 does not project itself anteriorly as in morphotype 1, where it is part of the curvature of the anterior margin.

The strong concave curvature of the pubic apron (typical of morphotype 1) follows normally its way up to the base of the iliac pedicle. There, reaching the level of the scar for the *ambiens* muscle (which is rugose and well marked), the anterior margin of the iliac pedicle changes direction abruptly, going straight upwards, until reaching its upper anterior corner. As a result, the anterior margin of the iliac pedicle assumes a vertical, straight, profile in lateral view (*Fig.* 36 – C and E). Another exclusive trait of morphotype 3 is present in the iliac pedicle, that is mediolaterally enlarged, being broader and triangular in proximal view

(Fig. 36 – D). This trait is not found in the pubes of morphotypes 1 and 2. The iliac pedicle in morphotype 3 is well discernible from the acetabular portion of the pubis.

The two pubes assigned to morphotype 3 are very different in size, bearing several morphological traits of their own. They have been thus individually discussed in more detail.

MCT 1640-R (right) (Fig. 36 – C, D; Fig. 88): MCT 1640-R is almost the same size of MCT 1641-R and MCT 1675-R, and similar to them in overall shape. The presence of a long ridge running along the lateral surface of its pubic apron and the shape of its iliac pedicle allows its allocation within the morphotype 3 category.

The iliac peduncle of MCT 1640-R is very stout. Its anterior margin is not projected as in other pubes, but almost vertical, so that, in lateral view, its anterior upper corner displays a rather quadrangular outline. In anterior view, the stouter nature of the iliac pedicle of MCT 1640-R becomes more evident. It towers itself over the pubic apron as an almost rectangular structure, transversally expanded. The pubic apron is a little deflected medially, so that its upper margin is not fully horizontally set, but a little inclined, facing inwards.

In proximal view, the iliac pedicle of MCT 1640-R is not flattened as in other pubes of morphotypes 1 and 2. It displays, instead, a triangular outline, in which the base faces outside and the vertex points medially (Fig. 36 – D). The lateral base of this triangle is a little concave. Its surface is rugose and marked by grooves. The acetabular portion is a little beveled laterally. The pubic foramen of MCT 1640-R is almost closed, and does not differ from the others.

MCT 1677-R (left) (Fig. 36 – E; Fig. 91): from all the pubes that compose the material, this is the second in size. Its distal end is broken and lost. Its pubic foramen is completely closed, suggesting it belonged to an adult individual (McINTOSH, 1990: 369). The typical features of morphotype 3 are highlighted in MCT 1677-R, probably because of its greater size and older state of maturity. It has its own features, however, which may be also related to its greater size.

In lateral view, the iliac pedicle projects itself upwards, surpassing the level of the acetabular portion of the pubis, forming with the latter a stair-step. The acetabular portion of the pubis is proportionally more developed in this large pubis, being longer than the length of the iliac pedicle. In proximal view, the acetabular portion of the pubis and the iliac articular surface are both deeply concave, and well separated one from the other by an

osseous bar. This bar is in fact a thickened border that surrounds the iliac pedicle, which is triangular in outline.

All morphological traits of MCT 1677-R seem exaggerated in relation to other, smaller pubes. The ischial pedicle, although laminar, is proportionally thicker, and the lateral ridge of the pubic apron is stronger and higher. The *ambiens* scar is well developed, and a bit prominent. The pubic foramen is large, placed far from the acetabular margin, at a distance equal to its length.

In posterior view, the ischial articular surface and the pubic symphysis are strongly S-curved. The pubic apron bears on the posterior margin, distally, a transversally wide and flattened area, probably for the articulation of the pubis mate.

Morphotype uncertain

Material: MCT 1611-R

MCT 1611-R (left) (Fig. 93): this bone is just a fragment of the distal part of a pubic apron and lacks diagnostic features. It is not possible to tell for sure to which morphotype it belongs.

Comparisons within morphotypes:

The pubes MCT 1641-R and MCT 1675-R (morphotype 1); MCT 1591-R and MCT 1592-R (morphotype 2); and MCT 1640-R (morphotype 3), are almost the same size. This is evidence that the morphological features displayed by those bones reflect the existence of at two or three different species in the sample. Morphotype 2 is different enough from morphotypes 1 and 3 to be considered a different species. Morphotypes 1 and 3, however, are more similar to each other, differing mainly in the construction and stoutness of the iliac pedicle, a trait that could be interpreted either as intraspecific variation or sexual dimorphism. The unique morphological traits displayed by the largest pubes of Peirópolis (MCT 1677-R and MCT 1711-R) may be related to size and age, since these two pubes belonged to adult species, as attested by their completely closed pubic foramina.

Comparisons with other taxa:

The Peirópolis pubes have been compared with the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Alamosaurus sanjuanensis*; *Andesaurus delgadoi*; *Antarctosaurus giganteus*; *Antarctosaurus wichmannianus*; *Gondwanatitan faustoi*; *Laplatasaurus araukanicus* (=*Titanosaurus araukanicus*); *Laplatasaurus sp.* (=*Antarctosaurus sp.)*; *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Rocasaurus muniozi*; *Saltasaurus loricatus*; *Titanosaurus australis* (=*Neuquensaurus australis*); *Titanosaurus colberti* and *Titanosaurus robustus* (=*Neuquensaurus robustus*).

The left pubis of the *Andesaurus delgadoi* (holotype MUCPv 132) is different from all pubes from Peirópolis (CALVO & BONAPARTE, 1991, fig. 6). It has a shorter pubic apron, and the articular area for the ischium is much longer in relation to overall length. The pubic apron lacks the prominent lateral ridge typical of morphotype 1 pubes. The anterior margin of the bone bears neither a slope, nor a prominence, distinguishing it from morphotype 2 pubes. The iliac pedicle is also transversally flattened, lacking, in proximal view, the typical triangular outline of morphotype 3 pubes (personal observation). Its anterior margin is not straight as in morphotype 3, but anteriorly projected, being continuous with the anterior margin of the pubic apron, being similar to morphotype 1 MCT 1641-R and MCT 1675-R pubes. There is no hook-like projection bordering the proximal anterior corner (distinguishing it from MCT 1711-R). A second right pubis of *A. delgadoi* (MUCPv-271) remains undescribed, but previous analysis indicate that it has the same morphology as the type species (CALVO, 1999: 22)

The left pubis of *Rocasaurus muniozi* (holotype MPCA-Pv 46) differs from all pubes of Peirópolis by the extremely forward projection of the pubic apron, and by the presence of a dorso-lateral expansion set at its distal end. Some traits further separates the pubis of *R. muniozi* from both morphotypes 1 and 2 of Peirópolis: the longitudinal lateral ridge is absent, and the anterior margin of the iliac pedicle bears no prominence or slope (SALGADO & AZPILICUETA, 2000: fig. 9d). The development of the iliac pedicle cannot be evaluated from given figures, so it is not possible to say if has a triangular outline in proximal view (as in morphotype 3). *R. muniozi* lacks an anterior hook-like process. The pubic foramen is large, oval and placed just behind the iliac pedicle, similar to the Brazilian pubes (SALGADO & AZPILICUETA, 2000: fig. 9d).

The pubis of *Opisthocoelicaudia skarzynskii* (ZPAL MgD-I/48 – holotype) is stout, with a long and massive shaft. Its external surface is rather concave, with a longitudinal convexity extending distally over the posterior margin of the shaft (BORSUK-BIALYNICKA, 1977: 33), but it is not clear if it is similar to the lateral ridge found in morphotypes 1 and 3. The space for the muscle *puboischiofemoralis externus* seems to be more restricted than in the Brazilian morphotypes 1 and 3, and the articular surface for the ischium is vertically oriented, instead of following a descending angle, as in the bones from Peirópolis (BORSUK-BIALYNICKA, 1977: fig. 12).

The anterior border of the pubis of *O. skarzynskii* does not slope as in morphotype 2 pubes, but at least a prominent tuberosity for the attachment of the muscle *ambiens* is present (BORSUK-BIALYNICKA, 1977: 33). The anterior margin of the iliac pedicle is not continuous with the anterior curve of the pubic apron, but abruptly changes direction upwards, becoming more straight and vertical (BORSUK-BIALYNICKA, 1977: fig. 12). This trait is similar in morphotype 3, but the Brazilian bones have a higher iliac pedicle, set at the same level (MCT 1640-R) or higher (MCT 1677-R) in relation to the plane of the acetabular portion of the pubis. In *O. skarzynskii*, the iliac pedicle slopes down a little in relation to the level of the acetabular floor, probably because of the over-development of the pubic pedicle of the ilium (BORSUK-BIALYNICKA, 1977: fig. 12).

The shape of the iliac pedicle in proximal view cannot be accessed in the ossified pelvis of *Opisthocoelicaudia*, but it is undoubtedly transversally wide (BORSUK-BIALYNICKA, 1977: 33), a trait also present in morphotype 3. There is no hook-like projection on the anterior border of the pubic pedicle, distinguishing it from MCT 1711-R.

The pubis of *Saltasaurus loricatus* shows both differences and similarities with the pubes of Peirópolis. The pubic acetabular portion and the ischial pedicle are set more medially than the iliac pedicle (POWELL, 1992: 194), while in the Brazilian pubes they are set at the same line. The anterior margin of the iliac pedicle bears neither a prominence, nor a slope, being easily separated from morphotype 2 pubes. There is no sign of an anteriorly projected hook-like process, distinguishing it from MCT 1711-R.

Among the similarities are the transversally development of the iliac pedicle (POWELL, 1992: fig. 35) and the presence of a strong longitudinal elevation on the ventral (lateral) surface of the pubis, which may be similar to the longitudinal lateral ridge found in morphotypes 1 and 3. This latter character is present only in PVL 4017-95, and it was considered as a morphological variation, that could be related to either sexual dimorphism

or the possibility of its belonging to another different sauropod species (POWELL, 1992: 194).

The left pubis of the holotype of *Titanosaurus colberti* (ISIR335/63) lacks a prominence marking a slope on the anterior margin of the iliac pedicle, being distinct from morphotype 2, displaying, however, a small elevation on the anterior margin (JAIN & BANDYOPADHYAY, 1997: fig. 24). It resembles morphotypes 1 and 3 by possessing a strong ridge running obliquely and anterolaterally along its shaft (JAIN & BANDYOPADHYAY, 1997: 125). It also shows a broad iliac pedicle, although it is not triangular as in morphotype 3 pubes, being rather subovate (JAIN & BANDYOPADHYAY, 1997: 125). The pubes of *T. colberti* further differ from the Brazilian ones by the shape of their distal ends, which are transversely swollen in the Indian species (JAIN & BANDYOPADHYAY, 1997: fig. 24c). The ischiadic symphyseal portion of the pubis of *T. colberti* is thin, extending almost to the midlength of the bone (JAIN & BANDYOPADHYAY, 1997: 125). This trait is not present in the Brazilian pubes, whose ischial articular areas (when fully preserved) are restricted to the upper third of the bones.

There are several titanosaurid species whose pubes are too much incomplete to allow good comparisons with the Peirópolis bones. The incomplete left pubis attributed to *Alamosaurus sanjuanensis* lacks both iliac and ischial pedicles, which are broken and lost (LUCAS & HUNT, 1989, fig. 5d). The anterior margin of the pubic apron is reminiscent of morphotype 1 by its curvature.

The pubes attributed to *Antarctosaurus wichmannianus* (MACN 6904 – holotype) and *Antarctosaurus giganteus* (MLP/AC 2300) are too much incomplete HUENE, 1929). Similarly, a fragmented pubis of the hypodigm of *Lirainosaurus astibiae* (MCNA 7467) was reported (SANZ *et al.*, 1999), but was neither figured, nor described in the text, hindering any comparison with the Brazilian material.

Also difficult to compare are the pubes of *Titanosaurus australis* and *Titanosaurus robustus*. The first is represented by three pubes of the hypodigm (MLP/CS 1263, 1102, 1304) which are incomplete (HUENE, 1929: lam. 13, fig. 6 and lam. 14, figs. 1 and 2, respectively). Nevertheless, the pubes of *T. australis* are more similar to morphotype 1 in having a continuous curved anterior margin. They lack a slope on the base of the iliac pedicle, distinguishing them from morphotype 2. They are also different from morphotype 3 in lacking a vertical deflection of the anterior margin. It is not possible to evaluate,

however, whether the pubis of *T. australis* had a similarly expanded iliac pedicle or not, for the bones were not figured in proximal view. The right pubis attributed to *Titanosaurus robustus* (Av. 2066) was not figured, but it was considered similar to that of *T. australis*, not capable of being properly separated from the later (HUENE, 1929: 51). For that reason, it is possible that the pubis of *T. australis* may be more similar to morphotype 1 than to morphotypes 2 and 3.

Both pubes of *Gondwanatitan faustoi* (MN 4111-V – holotype) are represented only by their middle portions. Unfortunately, the incomplete material hinders the association of *G. faustoi* to a single morphotype. Nevertheless, on its lateroventral surface, there is a strong and blunt bony ridge that disappears distally (KELLNER & AZEVEDO, 1999: 132). The presence of such a feature suggests that the pubis of *G. faustoi* may fall into either morphotypes 1 or 3.

The incomplete left pubis of *Laplatasaurus araukanicus* (hypodigm MLP/CS 1059) allows just superficial comparisons with the Brazilian material. Nevertheless, the absence of an anterior slope on the anterior margin of the iliac pedicle distinguishes it from morphotype 2 (HUENE, 1929: lam. 25, fig. 17a). The iliac pedicle in the pubis of *L. araukanicus* is transversally expanded (HUENE, 1929: lam. 25, fig. 17 d), being similar to morphotype 3. The right pubis attributed to *Laplatasaurus sp.* (PVL-3670-10) is too much incomplete, but the presence of a longitudinal elevation over its postero-ventral surface (POWELL, 1979: 196) suggests some affinities with morphotypes 1 or 3.

The pubis of the holotype of *Aelosaurus rionegrinus* (MJG-R 1) was not figured in the original description (POWELL, 1987b). The following comparisons were made based on some photographs (taken by A. Kellner). The pubis of *Aelosaurus rionegrinus* is a stout bone, with a over expanded distal end, differing in this respect from all other pubes from Peirópolis. The iliac pedicle is transversally expanded in proximal view, resembling morphotype 3, but it is somewhat quadrangular in outline. An additional specimen (MPCA-27174) was referred to *Aelosaurus sp.* (SALGADO & CORIA, 1993a: fig. 8). Its left pubis is similar to those Brazilian pubes of morphotype 1 and 3 in having a longitudinal elevated ridge running along the pubic apron. The ridge marks the division of the apron in two planes, the ventral one being concave, forming a well developed insertion area for the muscle *puboischiofemoralis externus* (SALGADO & CORIA, 1993a: 124). Unfortunately, the iliac pedicle of the bone has not been preserved, hindering any further

comparisons with morphotype 3 category. Nevertheless, this is the pubis that has shown the closest similarities with at least 2 morphotype categories from Peirópolis.

Characters of the pubis described in previous Sauropod phylogenies:

There are only three characters described in the literature concerning the sauropod pubis.

WILSON & SERENO (1998) defined two characters for the pubis: orientation of the pubic apron (character n° 46 of their analysis) and length of puboischial contact (character n° 95).

The first character has two states. The pubic apron may be either transverse (the primitive state) or canted posteromedially (the derived state). In theropods, prosauropods and *Vulcanodon*, the pubic apron is developed as a plate-shaped sheet of bone that extends transversely to meet its opposite along the midline. The apron, thus, has a transverse orientation. In eusauropods, in contrast, the surface of the blade curves more gradually away from the transverse orientation of the pubic foot and toward the posteriorly directed ischial peduncle. As a result, most of the apron is canted posteromedially and has a V-shaped cross-section at midlength (WILSON & SERENO, 1998: 40).

This character, unfortunately, is synapomorphic at a very basal level - that of the Eusauropoda. This taxon includes all sauropod dinosaurs except *Vulcanodon karibaensis*. The character is thus present in almost all sauropods, including the Peirópolis ones, being not useful in an analysis within the Titanosauridae.

The second character described by WILSON & SERENO (1998: 51, character n° 95) concerns the length of the puboischial contact. According to those authors, the primitive condition is present in eusauropods, in which the ischium and pubis meet below the acetabulum along a dorsoventral contact, which represents approximately one-third of the total length of the pubis, as measured from the iliac peduncle to the pubic foot. In *Camarasaurus* and Titanosauriformes (which display the derived state), the puboischial contact is relatively much deeper, constituting nearly half the total length of the pubis (WILSON & SERENO, 1998: 51). In *Camarasaurus* and *Andesaurus*, the length of the ischial peduncle of the pubis is 45% the total length of the pubis, whereas it makes up more than 50% of the total length of the pubis in *Brachiosaurus*. The condition in several titanosaurids is unknown because the margins of the ischial process of the pubis are

incomplete. (WILSON & SERENO, 1998: 51). So is the case among the Peirópolis pubes, so it is difficult to access the character in the material (with the exception of MCT 1592-R, which is completely preserved).

This character is related to the ischial character n° 13 of SALGADO *et al.* (1997a), which will be discussed in the next chapter.

The third character concerning the pubis was defined by SALGADO *et al.* (1997a, character n° 24), and refers to pubis length. According to those authors, the length of the pubis (measured from the midpoint of the pubo-ischiatic symphysis to the distal ends of both pelvic bones) is primitively subequal or shorter than the length of the ischium in primitive theropods, basal sauropodomorphs, and all non-titanosaur sauropods (such as *Brachiosaurus brancai*, Camarasauridae, Diplodocidae, *Barapasaurus tagorei* and *Vulcanodon karibaensis*) (SALGADO *et al.*, 1997a: 20). The derived condition, in which the pubis is longer than the ischium, is present in the Titanosauria (a clade comprising *Andesaurus delgadoi* plus the Titanosauridae), and is considered a synapomorphy for that taxon (SALGADO *et al.*, 1997a: 20).

This character, different from the previous two, is useful to diagnose the Peirópolis material at least at the Titanosauria level. Although the derived condition could be confirmed only directly in articulated material, or in associated material of only one individual (none of which is the case of the disarticulated, scattered Peirópolis bones), indirect observations point to its presence in our sample, since the largest of all ischia found (the 40 cm long MCT 1689-R) is shorter than the smallest pubis found (the 50 cm long MCT 1675-R).

ISCHIUM

The ischium is one of the three pelvic bones. It is positioned ventrally to the ilium and posteriorly to the pubis, also contributing to the formation of the acetabulum. In dinosaurs plesiomorphically, the ischium is about the same length of the femur (RASSKIN-GUTMAN, 1997: 539). It is straight and elongated in prosauropods (McINTOSH, 1990:370).

In primitive sauropods (*Vulcanodon* and *Barapasaurus*), the ischium is straight and still longer than the pubis (McINTOSH, 1990: 376). In more advanced sauropods, the ischium turns to a shorter bone, which is, at best, equal to the pubis in length. The shaft is typically directed caudoventrally. The manner of articulation of the distal ends (which are

sometimes fused) varies considerably among different sauropods. In *Haplocanthosaurus*, *Camarasaurus*, *Opisthocoelicaudia*, and *Brachiosaurus*, the twisted shafts of the ischia and their narrow distal ends meet edge to edge. In *Brachiosaurus* the shafts and distal ends are broader, and the ischium is directed more nearly vertically. In diplodocids, the distal ends are greatly expanded in both directions, and the ischia meet more nearly side by side (McINTOSH, 1990:370).

In cetiosaurids, the ischium is slender and only slightly expanded distally in *Cetiosaurus*, *Haplocanthosaurus*, and *Shunosaurus* (McINTOSH, 1990: 379).

In the Camarasauridae (represented by *Camarasaurus*) and in the Brachiosauridae (represented by *Brachiosaurus*), the slender blade of the ischium is directed backward and downward, and similarly twisted to meet its mate edge to edge distally (McINTOSH, 1990).

In the Diplodocidae Diplodocinae, the distal ends of the ischia meet side by side, and are dorsoventrally thickened to a greater extent in *Apatosaurus* than in any other sauropod (McINTOSH, 1990:391). In *Diplodocus*, the ischia have a slender shaft, which expands and thickens distally, so that the meeting of the two ischia is intermediate between the side-by-side arrangement of *Apatosaurus* and the edge-to-edge articulation of *Camarasaurus* and *Brachiosaurus*. (McINTOSH, 1990:389). In *Dicraeosaurus*, the distal end of the ischium is broadened dorsoventrally to articulate with its mate side by side (McINTOSH, 1990: 393).

In the Titanosauridae, the ischia are short in *Opisthocoelicaudia* and *Saltasaurus*, and have a well-developed head in the latter (McINTOSH, 1990: 395). In *Alamosaurus*, the ischia have broad shafts and are united edge to edge for their entire length. The distal ends are broad but thin (McINTOSH, 1990: 396). The ischium of *Antarctosaurus* differs from that of *Alamosaurus* by having a long slender shaft and by being not broad at the distal end (McINTOSH, 1990: 397).

The ischium is the site of attachment of some important muscles of the hind limb (BORSUK-BIALYNICKA, 1977: fig. 12 and 17), but only the two most important are considered herein: the *puboischiofemoralis externus* (pife) and the *flexor tibialis* (flt) (Fig.10). The former occupies the anterior inferior surface of the shaft, extending itself anteriorly to meet the femur and the pubis. The *flexor tibialis* inserts at mid-length of the ischium shaft, on its inferior surface, near the posterior margin. From that point, it descends to insert into the posterior margin of the tibial head.

General observations:

Seven ischia have been recovered from Peirópolis deposits (Tables 30 and 31, Fig.18). They do not vary too much in size (Fig. 101 – A to E).

Two of them have come from "Serra da Galga" (MCT 1585-R and MCT 1586-R). They are in excellent state of preservation, specially MCT 1586-R. These two bones are the same size, display the same morphology and form a perfect pair, suggesting that they have belonged to a single individual.

There are three ischia recovered from "Site 1" (MCT 1654-R, MCT 1655-R, and MCT 1661-R). MCT 1654-R (left) is broken at the distal end, and is almost the same size of MCT 1661-R. MCT 1655-R (right) has more or less the same dimensions as the ischia from "Galga", but is different in morphology. It is in good state of preservation. MCT 1661-R (left) is larger than MCT 1655-R. Its shaft is complete, but a great part of its pubic pedicle is broken and lost. It is, however, morphologically similar to MCT 1655. It is possible that one of them, or both, have belonged to one of the two pelves found there.

There are two more ischia among the material (MCT 1679-R and MCT 1689-R), but their exact site of origin is unknown. They have been recorded as "Peirópolis surroundings". MCT 1679-R (right) is incomplete, lacking the distal end. The pubic pedicle is too damaged and incomplete. The iliac pedicle is also severely eroded. It shares a morphological trait with MCT 1654-R, suggesting its association with "Site 1" (this will be discussed later). MCT 1689-R (right) is the largest of all ischia. The articular border is damaged, but it in fairly good state of preservation. This bone is interesting for it displays an unique morphology among the Peirópolis material.

Morphology:

As the pubis, the proper orientation of the ischium in the sauropod pelvis lays on an oblique line which projects itself medially, as well as posteriorly, in a V-shaped manner. The distal part of the shaft suffers a violent twist in relation to the proximal part, in order to meet its mate and articulate with it along the ischial symphysis. In doing so, the distal blade assumes a more inclined position, with one surface facing downwards and laterally, and the opposite one facing upwards and medially. To standardize our descriptions, we have

considered the bone as a fully horizontal piece, parallel to the ground. The downwards-lateral surface is treated as the inferior surface. The upwards-medial surface is the superior surface. The anterior, or proximal, view envisages only the iliac pedicle. The medial side comprises both articular areas for the pubis and for the other ischium. The lateral side comprises the whole length of the ischial shaft. The distal view refers to the distal end of the ischial shaft only.

In superior view, the ischium has a typical hatchet-like shape, with the blade set medially, with the handles extending both anteriorly and posteriorly. The proximal end corresponds to the iliac pedicle (il ped) of the ischium. It is narrow and transversally expanded. The distal shaft (dst), which bears the articular area for the ischium mate - the ischial symphysis (is sym), is also narrow, but it is longer and lesser expanded than the iliac pedicle (Fig. 37).

The blade corresponds to the pubic pedicle (pu ped) of the ischium (Figs. 37, 38) It is a laminar and quadrangular structure, whose medial border articulates with the ischial pedicle of the pubis. Its anterior corner is squared. The posterior margin lacks a distinct corner, for the blade follows a convex curve to meet the medial border of the distal portion of the shaft. The surface of the blade is slightly concave, because of the external thickening of the whole shaft. The lateral margin of the ischium follows a strong concave curve. The distal shaft is laminar and flattened, and longer than the proximal one. The distal end is somewhat expanded, but not as much as the proximal end. The ischial symphysis is set at the medial border of the distal shaft, making it very thin. The lateral border is thicker, but still laminar in shape.

In inferior view the bone displays the same hatchet-like outline, but the ischial blade is concave. The distal shaft of the ischial pedicle is also a bit concave. But the most important feature of the inferior aspect of the ischium is the presence of a rugose muscle scar, set over a small lateral process (lat prc) (Fig. 37 – D; Fig. 38 – C, D). This elevation is placed at the middle of ischial shaft, near the lateral border of the bone, and is probably the insertion point for the muscle *flexor tibialis* (BORSUK-BIALYNICKA, 1977: fig. 12 and 17). The degree of development of this lateral process varies within the different ischia from a low elevation to a rather high, well developed prominence.

In medial view, the most striking features of the ischium are the iliac and the pubic pedicles (Fig. 37 – C, D). The iliac pedicle is an expansion set at the proximal end of the ischial shaft. It is transversally oriented, and twisted at about 60° in relation to the ischial shaft. The pubic pedicle is laminar and curved. Its anterior portion tapers gradually in

posterior direction, so that the lamina gets thinner distally. The curve is concave up, while the lower side is convex. The ischial symphysis is plate-like and thin. The lateral process for the muscle *flexor tibialis* may be clearly seen in this view.

In lateral view The bone do not show important morphological features. The lateral border is still laminar, but thicker than the medial one. A portion of the surface of the iliac pedicle may be seen in this perspective, as well as the lateral process for the *flexor tibialis*.

In proximal view, the iliac pedicle shows itself in full shape. It has a tear drop outline, with the curved side facing outside, and the pointed one facing inside (Fig. 37 – E; Fig. 38; Fig. 39).

In distal view the end of the ischial shaft is a flattened structure, laminar and asymmetrical in shape, for the medial border is thinner than the lateral border (Fig. 37 – F).

The ischia from Peirópolis are very similar to each other in respect to the proximal part of the shaft. They vary, however, in the morphology of their distal shafts, and this variation was the base to establish three different morphotypes within the material.

Morphotype 1

Material: MCT 1585-R and MCT 1586-R

Description: morphotype 1 is defined by having a medial reentrance, like an opened foramen, placed just at the beginning of the long and narrow distal shaft (Fig. 37 – A, B – med r). This reentrance is placed at the medial margin, and is ungual-shaped, with the tip oriented in anterior direction. Part of this foramen is formed by the posterior border of the pubic pedicle, which converges abruptly back in anterior direction. Behind the reentrance stays a convexity portion of the ischial symphysis, which is followed immediately by a concave curve. The only bones to show this morphology are those from "Serra da Galga". This reentrance resembles a similar feature present in the ischium of *Camarasaurus grandis* (WILSON & SERENO, 1998: fig. 29).

MCT 1585-R (left) (Fig. 95 – A, C, D, F, G) and MCT 1586-R (right) (Fig. 37; Figs. 38 – A and 39 – A, for comparison; Fig. 94; Fig. 95 – B, E; Fig. 97 – A, D - for comparison): they both display the medial reentrance typical of morphotype 1. The iliac pedicles are well developed, and extend over a greater length of the ischial shaft than in

morphotype 2. The reentrance is better seen in MCT 1586-R, due to the excellent state of preservation of its pubic pedicle, which is complete from the anterior corner to the distal border. The reentrance of its mate (MCT 1585-R) is less developed, but still visible, despite some damage of the distal border of the pubic pedicle. The process for the muscle *flexor tibialis* is distinct in both bones, and is placed near the lateral border of the shaft.

Character 36 of SALGADO *et al.* (1997a) reaches values of about 0.46 for both bones (less than 50%) indicating that these bones may not belong to a species within the *Alamosaurus* + Saltasaurinae clade.

Judging from its outline, one of these ischia (probably MCT 1585) was figured by McINTOSH (1990: fig. 16.15 V), based on a photo courtesy of L.I. Price.

Morphotype 2

Material: MCT 1654-R, MCT 1655-R, MCT 1661-R and MCT 1679-R

Description: morphotype 2 is similar to morphotype 1, differing from it only by lacking the medial reentrance (med r) described above. This morphotype has a shorter pubic pedicle than the anterior one, making its distal shaft longer (Fig. 38 – B, C).

The ischia of morphotype 2 show some variations, which are discussed below. Those that are most similar to each other have been lumped together to avoid repetition.

MCT 1655-R (right) (Fig. 38 – B, C; Fig. 39 – B; Fig. 97 – B, C, E, F) and MCT 1661-R (left) (Fig. 96 – B, E; Fig. 98): MCT 1655 is in good state of preservation. The process of the *flexor tibialis* is distinct, and shows the same degree of development as in "Serra da Galga" ischia. This process, however, is placed at some distance from the lateral margin (at about 1 cm). The evaluation of character n° 36 of SALGADO *et al.* (1997a), resulted in the following value: 0.42, which is less than that value found for the two previous ischia.

MCT 1661-R is a little bit longer than MCT 1655-R, and lacks much of the pubic pedicle, which makes its allocation in morphotype 2 a little uncertain. Nevertheless, the preserved part of the distal shaft seems to be uniform in width, lacking the medial reentrance of morphotype 1. The *flexor tibialis* process is also set at some distance from the lateral border. The evaluation of character n° 36 of SALGADO *et al.* (1997a), resulted in the

following value: 0.41, which is similar to that found in MCT 1655. The presence of these traits in common with MCT 1655-R, was decisive to classify MCT 1661-R as a morphotype 2 ischium.

MCT 1679-R (right) (Fig. 99) and MCT 1654-R (left) (Fig. 38 – D; Fig. 96 – A, C, D): the iliac pedicle of MCT 1679-R is too eroded, and the distal shaft is incomplete, being distally broken. Nevertheless, the preserved part is complete enough to attest the absence of a medial reentrance, allowing its classification within morphotype 2. This bone is also more robust than others already described. Its *flexor tibialis* process is the most developed of all, being high, rugose and pointed.

MCT 1654-R has lost a great part of its pubic pedicle and all its distal shaft, making impossible its classification within any of the three morphotypes described. It shares with MCT 1679-R, however, the same well developed process for the *flexor tibialis* muscle (Fig. 38 – D). Only for this reason, it is here tentatively classified as morphotype 2.

Morphotype 3

Material: MCT 1689-R

Description: morphotype 3 is characterized by the wide and laminar shape of the distal shaft (Fig. 38 – E; Fig. 39 – C, D). It does not display the hatchet-like outline of the others because its pubic pedicle is continuous posteriorly with the distal shaft, so that the bone displays the same width from the anterior corner of the pubic pedicle to the medial corner of the distal end. The pubic pedicle is, nevertheless, distinct because it is thicker than the ischial symphysis and retains the normal curved morphology seen in other ischia. The typical reentrance that is found in morphotype 1 is absent.

MCT 1689-R (right) (Fig. 38 – E; Fig. 39 – C, D; Fig. 100): this ischium is unique in its morphology. Unfortunately, the exact site of origin is unknown, so it was recorded as "Peirópolis surroundings". It perhaps belongs to one of the titanosaurid pelves kept within the DNPM collection (*fid.* Diógenes Campos). The association of this ischium with one of those pelves would clarify its origin. All ischia from Peirópolis display a narrow distal shaft, which is slightly distally expanded. MCT 1689-R differs from all of them by possessing a wide distal shaft, in which the ischial symphysis is continuous with the

articular surface of the pubic pedicle (Fig. 39 – C, D). This gives the bone, just below the base of the iliac pedicle, a rather laminar shape.

The overall shape of MCT 1689-R is reminiscent of the Saltasaurinae kind of ischia. The evaluation of character n° 36 of SALGADO *et al.* (1997a) results in 0.47 - a higher value than those found for any of the previous specimens described. Nevertheless, it is still lower than the 50% necessary to include it within the *Alamosaurus* + Saltasaurinae clade, suggesting that this specimen could be more basal. The evaluation of this character, however, may fall in error, because it is difficult to take the measurements defined by SALGADO *et al.* (1997a) in a tridimensional, twisted bone such as the ischium. If MCT 1689-R proves to be a Saltasaurinae ischium, this would be the first record of this subfamily in Brazil. The process for the *flexor tibialis*, although present, is the less developed of all ischia studied, being reduced to a rugosity.

Comparisons within morphotypes:

The ischia from Peirópolis do not display much variation in size. The largest ones are MCT 1661-R and MCT 1689-R (the largest), and even these do not exceed the average size of the sample. For this reason, it is possible that the morphological variation found within the specimens is not a mere product of different ontogenetic states. This may reflect normal morphological variation of a population, variation related to sex, or even the existence of more than one species within the sample (Fig. 38). Morphotypes 1 and 2 are similar to each other, except for the presence of a medial reentrance in the ischial distal shaft. At the same time, this morphology is also widespread among titanosaurids whose ischia are known. This suggests that the morphotypes may represent only one species, in which the ischia varied from specimen to specimen, or were the result of sexual dimorphism.

Morphotype 3, however, is very different from the others, being very similar to a Saltasaurinae-like ischium. The difference in this case may reflect the existence of a second different species among the Peirópolis material.

Comparisons with other taxa:

The Peirópolis ischia have been compared with the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Alamosaurus sanjuanensis*; *Andesaurus delgadoi*; *Antarctosaurus wichmannianus*; *Gondwanatitan faustoi*; *Malawisaurus dixeyi*; *Opisthocoelicaudia skarzynskii*; *Rocasaurus muniozi*; *Saltasaurus loricatus*; *Titanosaurus australis* (=*Neuquensaurus australis*); and *Titanosaurus colberti*.

The ischia of the additional specimen of *Alamosaurus sanjuanensis* (USNM-15560) are different from all ischia from Peirópolis. It distinguishes itself from morphotypes 1 and 2 by the overall shape of its shaft, which is short and broad, with little expansion of the distal ends (GILMORE, 1946: 39). This contrasts immediately with the slender shafts of morphotypes 1 and 2 ischia, as well as with their transversally expanded iliac pedicles. There is no trace of a reentrance in the ischium of *Alamosaurus* (GILMORE, 1946: fig. 11). The distal shaft of the ischium of *A. sanjuanensis*, although wider than in morphotypes 1 and 2, is still less wide than in morphotype 3. Besides, the distal shaft is short, its length making less than 50% of the length of the articular portion of the bone (including the iliac pedicle) (GILMORE, 1946: pl. 10; SALGADO *et al.* 1997a: 23). In all Brazilian ischia, even in MCT 1689-R, the distal shafts are longer. The American species shows a stronger curvature along its posterior margin, and the articular margin for the pubis is proportionally longer. It is not clear whether the prominence for the *flexor tibialis* was present or not.

The left ischium of *Andesaurus delgadoi* (holotype MUCP-v 132) may be promptly distinguished from both morphotypes 1 and 2 by the shape of its distal shaft, which bears a very wide blade (CALVO & BONAPARTE, 1991: fig. 5a). In this respect, it resembles MCT 1689-R (morphotype 3). But the ischium of *A. delgadoi* shows still more differences in relation to the Brazilian material: the iliac pedicle is less developed, being shorter and narrower, and the prominence for the muscle *flexor tibialis* is absent. The pubic symphysis is also longer, making about 50% of the total length of the ischial shaft, while this relation in Brazilian ischia makes 40% in MCT 1586-R (morphotype 1) to 35% in MCT 1689-R (morphotype 3).

The ischium of *Rocasaurus muniozi* (holotype MPCA-Pv 46, fig. 9 c) may be easily separated from morphotype 1 and 2 ischia by the lack of a medial reentrance and by its wider distal shaft. It is not as wide as in MCT 1689-R (morphotype 3). The ischium of *R. muniozi* is also strongly curved backwards, so that the iliac pedicle and the distal ischial shaft are set at right angles one in relation to the other SALGADO & AZPILICUETA,

2000: fig. 9 c), a trait absent in the uniform gradually curved Brazilian ischia. The lateral process for the insertion of the muscle *flexor tibialis* is absent in the Argentinean species.

The ischium of *Saltasaurus loricatus* (PVL 4017-99 – hypodigm) differs from morphotypes 1 and 2 by having a distal ischial shaft short and widely expanded, instead of the long and narrow shafts of the Brazilian bones POWELL, 1992: fig. 36). The distal shaft of the ischium of *S. loricatus* resembles morphotype 3, but differs from it by the proportions of the whole shaft. In *Saltasaurus*, the proximal portion, containing the iliac and pubic pedicles and the acetabular portion make more than half of the total length of the bone (POWELL, 1992: 195). This proportion in Brazilian MCT 1689-R (morphotype 3) is less than 50%. There is a longitudinal prominence for muscle insertion near the posterior margin of the ischium of *Saltasaurus* (POWELL, 1992: 195). This prominence may be the insertion for the *flexor tibialis*, which is also present in all ischia from Peirópolis.

The ischium of *Titanosaurus colberti* (holotype ISIR335/65) is promptly distinguished from morphotypes 1 and 2 by the width of its distal shaft (JAIN & BANDYOPADHYAY, 1997: fig. 25). It may be also distinguished from morphotype 3, whose ischial symphysis has the same width as the pubic pedicle, while in *T. colberti*, the width of the pubic blade still exceeds the width of the distal shaft a little. This last is also shorter in relation to the total articular portion of the bone, making less than 50% of its total length. The pubic pedicle bears a knob on its upper corner (JAIN & BANDYOPADHYAY, 1997: fig. 25) which is not present in any of the Peirópolis bones. The prominence of the *flexor tibialis* is either absent or poorly developed.

The left ischium of *Malawisaurus dixeyi* (additional material – MAL 142) is immediately distinguished from morphotypes 1 and 2 ischia from Peirópolis by the shape of its distal shaft, which is very wide, differing from the narrow and slender shafts of these morphotypes (JACOBS *et al.*, 1993: fig. 1 g). Although a wide shaft is present in morphotype 3, *M. dixeyi* may be differentiated from it by the development of the iliac pedicle, which is less transversally expanded in the African species as in the Brazilian specimen. In fact, this part of the bone resembles *Andesaurus delgadoi*, from Argentina. The acetabular portion of the ischium seems to be less concave than in the majority of titanosaurids, resembling the ischium of *Aelosaurus sp.* in this aspect. The presence or absence of a prominence for the *flexor tibialis* cannot be confirmed in *M. dixeyi* by the given figure.

The ischium of the holotype of *Opisthocoelicaudia skarzynskii*, with its narrow and long distal shaft, resembles morphotypes 1 and 2 from Peirópolis, in overall shape

BORSUK-BIALYNICKA, 1977: fig. 12). The posterior border is, however, strongly curved, so that the distal shaft is set almost at a right angle in relation to the iliac pedicle. The acetabular margin of the ischium is also curved, and the iliac pedicle is asymmetrical, for the upper margin (which contributes to the floor of the acetabulum) is shorter than the lower margin (whose lower anterior corner contacts the pubis). This difference seems to be an accommodation of the pubic pedicle influenced by the strong backward turn experienced by the distal shaft of the ischium. The prominence for the *flexor tibialis* is present, but displaced a little downwards. The ischium of *Opisthocoelicaudia skarzynskii* clearly distinguishes itself from morphotype 1 by lacking the typical medial reentrance placed on the distal shaft.

Some Titanosauridae species have a ischium that is similar to morphotype 2 in overall shape, bearing a similarly narrow distal shaft.

The ischium of a specimen referred to *Aelosaurus sp.* (MPCA-27174) resembles, in overall shape, the morphotypes 1 and 2 from Peirópolis (SALGADO & CORIA, 1993a: fig. 9 and lam. 1 h). The pubic pedicle is laminar, and the distal shaft is long and narrow. The presence of a reentrance placed at the medial border of the distal shaft cannot be properly evaluated for the bone is a little damaged at that portion (SALGADO & CORIA, 1993a: fig. 9). The iliac pedicle is shorter and the acetabular margin is less concave than in the Brazilian forms. The presence of a prominence for the *flexor tibialis* cannot be confirmed by the given figures.

The ischium of the holotype of *Aelosaurus rionegrinus* were not figured in the original description (POWELL, 1987b). The available drawing is too schematic to allow comparisons (SALGADO & CORIA, 1993a: fig. 10 e). Nevertheless, the outline of the bone is similar to morphotype 2, by having an acetabular margin as concave as the Peiropolis material, and by lacking the reentrance typical of morphotype 1.

The ischium of *Antarctosaurus wichmannianus* (MACN 6904 – holotype) is similar in overall shape to morphotype 2. This bone has a hatchet-like outline, and bears no reentrance in the distal shaft. This last is rather triangular in distal view (HUENE, 1929: lam 32, fig. 3c), instead of being rectangular and planar as in all Brazilian ischia.

The ischia of the holotype of *Gondwanatitan faustoi* (MN 4111-V) are similar in general morphology to the Peirópolis ischia (KELLNER & AZEVEDO, 1999: fig. 19). They are, however, too damaged, and therefore, cannot be referred with certainty neither to morphotype 1, nor to morphotype 2. The preserved parts of the distal shafts, however,

show that they are different from morphotype 3. The prominence for the muscle *flexor tibialis* is present.

There is only one Titanosauridae species with a ischium similar to Brazilian morphotype 3 - *Titanosaurus australis*.

The left ischium of *Titanosaurus australis* (hypodigm MLP/CS 1261) differs from morphotypes 1 and 2 by the shape of its distal shaft (HUENE, 1929: lam. 14, fig. 3), The distal shaft is short and laminar, and the ischial symphysis is as wider as the pubic symphysis. In this respect, the ischium of *T. australis* is the most similar to morphotype 3. However, its pubic pedicle is not fully laminar, but has a plate-like, wide and flattened anterior border (HUENE, 1929: 41). This trait is not present in any of the Brazilian bones. The lateral margin of the shaft is strongly curved, and a long muscle scar is present near the lateral border. This scar may be the insertion point of the *flexor tibialis*, but HUENE (1929: 41) considered it the *adductor femoris*.

Characters of the ischium described in previous Sauropod phylogenies:

Several characters of the ischium have been described in the literature, and are herein discussed:

WILSON & SERENO (1998) described three characters of the ischium. Two are basal for sauropods: ischial blade length (character n° 8) and shape of ischial distal shaft (character n° 9), each one with two states. The third character, cross-sectional shape of the ischial distal shafts (character n° 88) is synapomorphic for their Macronaria.

According to those authors, the ischial shaft may be shorter (the primitive condition) or equal to or longer than the pubic shaft (the derived condition). In prosauropods and theropods, the shaft of the pubis is moderately to markedly longer than the shaft of the ischium. In prosauropods, the pubic blade is approximately 15% longer than the shaft of the ischium, with the latter measured from the base of the obturator expansion. A similar proportion is found in allosauroid theropods, although the differential in length is often considerably greater in other theropods (WILSON & SERENO, 1998: 27).

In sauropods, the shaft of the ischium is as long as or longer than the shaft of the pubis. These altered proportions are largely the result of shortening of the length of the pubic shaft relative to the base of the pubis, because the overall length of the pubis is usually equal to, or greater than, that of the ischium. The derived length of the ischial shaft is present in the

basal titanosauriform *Euhelopus*, but the shaft is shorter than the pubic shaft in all titanosaurs, which have markedly reduced the overall size of the ischium (WILSON & SERENO, 1998: 27).

This character is similar to a pubic character described by SALGADO *et al.* (1997a: character n° 24), which regarded the shortening of the ischial shaft as a synapomorphy of the Titanosauria (SALGADO *et al.*, 1997a: 20).

This character should be used with caution, since its distribution varies among several groups of the Saurischia. SALGADO *et al.* (1997a: 20) pointed out that pubes are primitively subequal or shorter than the length of the ischium in primitive theropods, basal sauropodomorphs, and all non-titanosaur sauropods; whereas WILSON & SERENO (1998: 27) said just the contrary, considering that in prosauropods and theropods, the shaft of the pubis is moderately to markedly longer than the shaft of the ischium. Nevertheless, both authors considered the reduction of the ischial shaft in relation to the pubic shaft independently developed in some derived theropod groups, such as Tyrannosaurids (SALGADO *et al.*, 1997a: 20) and the Allosauroidea (WILSON & SERENO, 1998: 27). The evaluation of the character may also suffer the influence of the way it is measured, whether the pubis is measured from the midpoint of the pubo-ischiatic symphysis to the distal ends of both pelvic bones (SALGADO *et al.* 1997a: 20) or the ischial length is measured from the base of the obturator expansion (WILSON & SERENO, 1998: 27).

The presence of this character in the Peirópolis material depends on findings of articulated material. But, as it was previously discussed (in the Pubis section), the indirect evidence hints at ischia which are shorter than the pubes.

WILSON & SERENO describe one more basal sauropod character of the ischium (1998: 27, character n° 9), concerning the shape of the ischial distal shaft. This may be either triangular with the depth of ischial shaft increasing medially (the primitive condition, present in prosauropods and theropods) or bladelike, with dorsoventrally flattened end, with medial and lateral depths subequal (the derived condition).

The character is clearly present is all ischia of Peirópolis, whose distal shafts are flattened and laminar. Unfortunately, this character state is a synapomorphy of the Sauropoda, and just helps to identify the Peirópolis material as belonging to a sauropod.

The third character discussed by WILSON & SERENO (1998: 50 - character n° 88) regards the shape of the ischial distal shafts. They may be either V-shaped, forming an angle

of nearly 50° with each other (the primitive condition) or flat, nearly coplanar (the derived condition).

According to those authors, the ischia of basal sauropods and diplodocids meet on an angle, forming a triangle in distal view. In *Apatosaurus* and *Dicraeosaurus*, for instance, the ischial shafts are somewhat twisted, so that the long axes of their distal extremes are oriented 30° to 35° from vertical (WILSON & SERENO, 1998: 50). In Macronaria (a clade uniting *Haplocanthosaurus*, *Camarasaurus* and Titanosauriformes), the dorsoventral depth of the medial and lateral extremes of the distal portions of the ischia are subequal, and the distal ischia twist nearly 90° from vertical to form a broad, nearly horizontal plate at their distal extremes. In *Brachiosaurus* and the basal titanosaur *Malawisaurus*, the ischial shafts are platelike and twist distally to form a nearly horizontal surface. This condition is present in *Andesaurus* and *Aelosaurus*, though the ischia are not as platelike. In more derived titanosaurs, the ischial shafts are much shorter than the pubic shafts, and although they are flattened, the ischial shafts do no twist quite as much distally (WILSON & SERENO, 1998: 50).

This condition is difficult to access in the Peirópolis ischia due to its disarticulated state. Nevertheless, their overall shape resembles that of above mentioned taxa, such as *Andesaurus* and *Aelosaurus*. So, the manner of articulation of the Peirópolis ischia may have been similar to those titanosaurids.

SALGADO *et al.* (1997a) defined two characters concerning the ischium: length of pubic articulation of ischium (character n° 13) and length of posterior process of the ischium (character n° 36).

The first character displays two states. The length of the pubic articulation of the ischium may be either short (the primitive condition) or long (the derived condition). According to those authors, ischia with dorsoventrally extended articular surfaces for the pubis - so that the distance from the upper corner of the pubic blade of the ischium up to the posterior border of the bone is shorter than the pubic articulation – is a synapomorphy of their Camarasauromorpha (a clade comprising the Camarasauridae and the Titanosauriformes) (SALGADO *et al.*, 1997a: 12).

This character is similar to pubic character n° 95 of WILSON & SERENO (1998 – length of puboischial contact), already discussed.

This character is present in all ischia from Peirópolis which are complete enough to allow more or less accurate measurements (MCT 1585 and 1586, from "Galga"; MCT 1655,

from "Site 1"). The uniform morphological similarity displayed by the material suggests that the character was present in all other ischia, which allows its allocation in the Camarasauromorpha.

The second character presented by SALGADO *et al.* (1997a – character n° 36) concerns the length of the posterior process of the ischium, and display two character states: long (primitive) or short (derived).

According to those authors, most sauropods have the posterior process of ischium relatively long, so that, the distance from the upper corner of the pubic blade of the ischium up to the proximal end of the iliac peduncle is less than 50 percent of the distance from the same point up to the distal end of the posterior process (SALGADO *et al.* 1997a: 24). That is, most sauropods display the primitive condition.

The derived condition, where the posterior process of the ischium is significantly shorter, is present only in their unnamed taxon VI, a clade comprising *Alamosaurus sanjuanensis* and the Saltasaurinae) (SALGADO *et al.* 1997a: 23).

This character was evaluated in the Peirópolis material. The results are listed in Table 32, and show that none of the most complete ischia measured bear the derived condition, denying any Saltasaurinae identity to the material. Nevertheless, the character shows some variation among the different bones, which may be related to different morphotypes.

The last character described in the literature for the ischium comes from the work of SANZ *et al.* (1999 – character n° 39), and concerns the shape of the ischial process of ischium. This character display three states, and may be scored as long and non-laminar (primitive), long and laminar (first derived state) or short and laminar (second derived state) (SANZ *et al.*, 1999: 248).

According to those authors, the primitive condition is present in the non-titanosaurid *Patagosaurus* and *Haplocanthosaurus*, and in the titanosauroid *Opisthocoelicaudia*. Whereas the long and laminar state is present only in *Andesaurus* (SANZ *et al.*, 1999: 248 – character/taxon data matrix).

The short and laminar state is considered by those authors as a synapomorphy of the Titanosauria, a clade comprising *Epachthosaurus*, *Saltasaurus*, *Argyrosaurus*, *Lirainosaurus* and the "Peirópolis titanosaur" (SANZ *et al.*, 1999: 252). The character, however, can be accessed only in *Saltasaurus* and *Epachthosaurus*, for the other species lack preserved ischia.

This character state is similar to character n° 36 of SALGADO *et al.* (1997a), discussed just above, and, as already mentioned, is not present among the ischia from

Peirópolis. Therefore, the inclusion of the "Peirópolis titanosaur" in the Titanosauria, as done by SANZ *et al.* should be based on the presence of other synapomorphies.

UPCHURCH (1995: 379) pointed out that the distal shaft of the ischium is particularly short (longitudinally) and wide (transversely) in the Titanosauridae. Among the Peirópolis ischia, this character is clearly present only in MCT 1689-R. In other ischia, the distal shaft, although short, is not so wide transversely (Fig. 37 - A).

FEMUR

In prosauropods, the femur is primitively bent, following a sigmoid curved. In the Sauropoda, the femur is straight, being the longest bone in the skeleton (except in the Brachiosauridae). It is always longer than the tibia and fibula, and expanded at both extremities, the proximal end a bit much than the distal one. The cross-section of the femur shaft varies from an almost circular to an oval shape, in which the transverse diameter is longer than the anteroposterior one. On the posterior face of the femur there is a prominent ridge that arises at midlength of the medial border, which represents a rudimentary fourth trochanter (McINTOSH, 1990: 370). This is the point of attachment of the muscle *caudifemoralis* (BORSUK-BIALYNICKA, 1977) (Fig. 10 - cf).

The head of the femur is almost set at a right angle to the shaft. It rises slightly above and is somewhat more expanded anteroposteriorly than the greater trochanter, which is placed on the lateral half of the proximal end of the bone. Except in primitive forms, there is no trace of a notch between the head and greater trochanter. The muscle *iliofemoralis* attaches onto the greater trochanter (Fig. 10 - il fem), spreading itself over the lateral border of the head of the femur (BORSUK-BIALYNICKA, 1977: fig. 17). The distal end of the femur bears two prominent condyles on the posterior face. The tibial condyle is the larger of the two (McINTOSH, 1990: 372). The femur differs from genus to genus in its overall robustness, and its length in respect to the length of the humerus and tibia varies among the different families (McINTOSH, 1990).

In *Vulcanodon karibaensis* the slender femur, retaining some primitive features, such as a reduced but well-marked lesser trochanter and a much more prominent fourth trochanter. The tibia:femur ratio is a relatively small 0.58 (McINTOSH, 1990: 376). In the Cetiosauridae *Shunosaurus*, the femur is straight and slender, and lacks a lesser trochanter,

which might be represented by a barely perceptible prominence. The tibia:femur ratio is 0.57 (McINTOSH, 1990: 379).

In the Diplodocidae Diplodocinae, the femur is slender in *Diplodocus*, reaching a tibia:femur ratio of 0.65 to 0.69. In *Apatosaurus*, the bone is robust and the tibia:femur ratio equals 0.60. In the Dicraeosaurinae (represented by *Dicraeosaurus*), the femur is less slender than in *Diplodocus*, and the shaft is nearly circular in cross-section. The tibia:femur ratio is 0.62 (McINTOSH, 1990). In *Camarasaurus*, a genus of the Camarasauridae, the tibia:femur ratio is less than diplodocids and greater than brachiosaurids (McINTOSH, 1990: 386).

In brachiosaurids and titanosaurids, the femur displays a sharp deflection on the proximal third of its lateral margin, which may represent the last trace of an otherwise missing lesser trochanter (McINTOSH, 1990: 370). In *Brachiosaurus* (representing the Brachiosauridae) the femur is shorter than the humerus, an exception among sauropods. The tibia:femur ratio equals 0.58 (McINTOSH, 1990: 381).

The femur in the Titanosauridae has its lateral upper third even more deflected medially than in the brachiosaurids. The tibia:femur ratio varies among the different genera. It is 0.65 in *Titanosaurus indicus* and 0.69 in *Aegyptosaurus* (McINTOSH, 1990: 395), being similar to those values found in the Diplodocidae. In *Opisthocoelicaudia*, the tibia:femur ratio equals 0.58, the same as in the brachiosaurid *Brachiosaurus*. The fourth trochanter of femur is situated uniquely below the middle of the shaft (McINTOSH, 1990: 388).

General observations:

Five femora compose the material under study (Tables 33 and 34, Fig. 19). All of them have different sizes, and cannot be paired.

MCT 1601-R is the smallest femur from Peirópolis, but is excellently preserved. It has been unearthed in "Serra da Galga" and is the only femur whose site of origin is known for sure. Two femora (MCT 1602-R and MCT 1604-R) have been recorded as from "Peiropolis surroundings". MCT 1602-R is excellently preserved, and displays a morphology of its own. MCT 1604-R is very damaged. The last femora (MCT 1693-R and MCT 1712-R) may have not come from Peirópolis, but from somewhere near Uberaba, so they have been recorded as "Peirópolis?". They are in good state of preservation. MCT

1712-R is larger than MCT 1693-R, and both bones are the largest femora within the material.

Morphology:

The sauropod femur does not bear distinctive diagnostic characters in general, varying from genus to genus in overall robustness (McINTOSH, 1990: 370). All femora under study herein are no exception, displaying the normal features also found in other sauropods in general (Figs. 40 and 41).

The shaft is straight, and the cross section of it is elliptical, with the transverse diameter being the longest. The bone is expanded in both extremities, but not symmetrically. In posterior view, the femoral head is a well developed and bears a medial, rounded expansion to fit into the acetabulum. The lateral margin is deflected medially in its upper third (a character typical of the Titanosauriformes, widespread among titanosaurid femora), forming a lateral bulge (lat blg) on the bone (Fig. 40 – A; Fig. 41 – B). The greater trochanter (gr trc) shows normal sauropod development, and it is placed well below the upper margin of the femoral head (Fig. 40 – A; Fig. 41 – B). The fourth trochanter (fo trc) is marked by a longitudinal, low ridge, placed medially at the base of the upper third of the shaft (Fig. 40 – A, B; Fig. 41 – A).

The bone retains more or less the same width along the shaft, expanding gradually along the distal quarter. There, the two condyles for the lower leg elements (tibia and fibula) are well developed and strongly built. The tibial condyle (tb cnd) is placed at the medial distal margin, and is the largest of the two. The fibular condyle (fib cnd) is placed near midlength, and is less developed than the former (Fig. 40 – D; Fig. 41 – C).

In medial view, the fourth trochanter is well visible as a convex elevation protruding posteriorly. The tibial condyle is well developed and beveled posteriorly also. In proximal view, the femoral head assumes a rather rectangular profile, with the medial portion being a bit more swollen (Fig. 40 – C). In distal view, the femur shows a trident-shaped profile, where the two medial prongs represent the tibial and the fibular condyles. The tibial condyle is longer and less wide than the fibular one. There is a deep concave curve between the two condyles. Both proximal and distal surfaces of the femora are rugose, covered by bumps and grooves.

The femora from Peirópolis have been segregated into two different morphotypes, based solely in overall robustness of the bone.

Morphotype 1

Material: MCT 1601-R, MCT 1693-R, MCT 1694-R and MCT 1712-R.

Description: morphotype 1 is characterized by the slenderness of the shaft of the femur (Fig. 40). This morphotype is the most common found among the femora from Peirópolis. These femora show some variations, however, which are discussed below.

MCT 1601-R (left) (Fig. 40; Fig. 102): this femur was found in "Galga", and its shaft is a little bit more constricted below its middle than in any other morphotype 1 femur. Perhaps this is a juvenile feature, since this femur is the smallest of all. From the two tibiae found in "Galga " deposits (MCT 1587-R and 1695-R), only MCT 1587-R has a compatible size to be associated to this femur. The tibia:femur ratio equals 0.60 in this pair of bones. This is less than the values displayed by *Titanosaurus indicus* (0.65) and *Aegyptosaurus* (0.69) (McINTOSH, 1990: 395), but is higher than the value calculated for *Opisthocoelicaudia* (0.58) (BORSUK-BIALYNICKA, 1977: 46). If compared with the humerus from "Galga" (MCT 1597-R), the humeral:femur ratio equals 0.82. This seems to be to high, for the same ratio equals 0.74 for *Titanosaurus indicus* (McINTOSH, 1990: 395) and just 0.72 for *Opisthocoelicaudia* (BORSUK-BIALYNICKA, 1977: 46). So, the association between these two bones is not plausible.

MCT 1693-R (right) (Fig. 104): is the second largest within the material. It displays the same general morphology of MCT 1601-R, but its shaft is not constricted, being otherwise uniform in width. The head of this femur is a bit more medially deflected than in other femora.

MCT 1694-R (left) (Fig. 105 - D): is so damaged that little can be said about it. It overall proportions hint to morphotype 1.

MCT 1712-R (left) (Fig. 105 – A, B, C): is the largest femur of all, surpassing a meter in total length. Although showing the typical morphotype 1 shape, it differs a bit from the other femora by an increase in its anteroposterior diameter, resulting in a less

elliptical cross section of the shaft. This difference may be the result of an increase in body size. The fourth trochanter, surprisingly, is not so strongly developed as it would be expected in a femur with such large size.

Morphotype 2

Material: MCT 1692-R

Description: in morphotype 2, the shaft is robust, being comparatively wider than in morphotype 1 (Fig. 41).

MCT 1692-R (right) (Fig. 41; Fig. 103): is the only femur to fall into the morphotype 2 category. The shaft of this bones is extremely thick in comparison with all other femora under study. The width of this makes 20% of its total length, while in other femora this value is less than 15%. The lateral bulge is strong and well marked, and, below it, the lateral margin of the shaft is nearly straight. In medial view, the fourth trochanter is more developed, and the femur shows an anterior swelling of the shaft, that extends itself from the base of the upper quarter to the beginning of the distal quarter of the bone. The posterior distal margin of this femur, just between the tibial and fibular condyles, is marked by a series of foramina, which are not present in any of the other femora.

Comparisons within morphotypes:

There is not much to say about the two morphotypes displayed by the femora from Peirópolis. Unless by the fact that the bones differ in overall robustness, they are alike in their morphologies. The difference, however, cannot be attributed to size adaptation, since the largest femora (MCT 1693-R and MCT 1712-R) are all of the slender type.

The existence of two morphotypes for the femora lies over two possible explanations: either sexual dimorphism or presence of two different species in the material. Sexual dimorphism in sauropods is difficult to be proved. The presence of more than one species in the material is more plausible, since differences in overall femur robustness have been recognized to vary from genus to genus (McINTOSH, 1990: 370). Besides, all data accumulated so far on the Peirópolis titanosaurids (POWELL, 1987a; CAMPOS &

KELLNER, 1999; the present work) points to the existence of at least two species within the Peirópolis bone collection.

Comparisons with other taxa:

The Peirópolis femora have been compared with the following taxa: *Aelosaurus sp.*; *Antarctosaurus brasiliensis*; *Antarctosaurus giganteus*; *Antarctosaurus wichmannianus*; *Chubutisaurus insignis*; *Laplatasaurus araukanicus*; *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Rocasaurus muniozi*; *Saltasaurus loricatus*; *Titanosaurus australis*; *Titanosaurus robustus*; and *Titanosaurinae from Guararapes*.

The femur is known in several titanosauriform specimens. They are all too much similar in morphology, however, and the morphological descriptions are usually restricted to their classification into either a slender or robust category.

Among the recorded remains of titanosaurids found in Brazil, there are fragments of femora associated to a Titanosaurinae found in Guararapes (state of São Paulo) and a distal portion of a left femur described as *Antarctosaurus brasiliensis* (ARID & VIZOTTO, 1971). From the former, only a fragment of a left femur has been recovered (LEONARDI & DUSZCZAK, 1977: fig. 4). The piece is too incomplete to make useful comparisons, but the authors have based their observations on the femur from "Galga" (*MCT* 1601-R). Therefore, this specimen is here classified within morphotype 1 category. The holotype of *Antarctosaurus brasiliensis* (GP-RD-2) is represented by the distal portion of a left femur. It is too incomplete to allow good comparisons with the material from Peirópolis, but the published photos (ARID & VIZOTTO, 1971: figs. 1-3) suggest that this femur is also slender, being similar to morphotype 1. This specimen is large (155 cm of estimated total length), and bears a proportionally well developed fourth trochanter.

Several titanosauriform specimens have femora, which are similarly slender to morphotype 1 from Peirópolis. The incomplete left femur of *Aelosaurus sp.* (MPCA 27100) is similar to morphotype 1, unless for the stronger development of its fourth trochanter (SALGADO, CORIA & CALVO, 1997b: fig.5). Also slender are the femora of the holotypes of *Antarctosaurus wichmannianus* (HUENE, lam. 33, fig. 1), and *Antarctosaurus giganteus* (MLP 23-316 – holotype). This trait is unexpected is *A. giganteus*, whose left femur (231 cm long) has a surprisingly slender shaft for a such

gigantic form (HUENE, 1929: lam 36, fig. 2). The femur of *Chubutisaurus insignis* (holotype MACN 18222) is strong, but nevertheless slender, being similar to MCT 1712-R is overall shape. The lateral bulge seems more prominent in the Argentinean specimen, however. The incomplete right femur attributed to *Laplatasaurus araukanicus* (MLP/Av. 1047) seems also to belong to the slender category (HUENE, 1929: lam. 26, fig. 3).

There are some titanosaurid species whose femora are not only slender like, but also seem to have a constriction in the distal part of the shaft, resembling, in this respect, the Brazilian femur MCT 1601-R from "Serra da Galga". They include *Rocasaurus muniozi* (MPCA Pv 56 - holotype), which may be distinguished from Brazilian bones by the greater medial development of its fourth trochanter (SALGADO & AZPILICUETA, 2000: fig. 9 a) and *Titanosaurus australis*, whose fourth trochanter seems to extend itself over a longer distance of the shaft than in Brazilian bones (HUENE, 1929: lam. 15, figs. 1 - MLP/CS 1118). The Spanish form *Lirainosaurus astibiae* is represented by a left femur (MCNA 7468 paratype) which is very slender (SANZ *et al*. 1999: pl. 6 a). The proximal margin of the femoral head seems highly placed in relation to the greater trochanter in that specimen than in the Brazilian femora.

The only species to have femora with robust shafts, being thus similar to morphotype 2 Brazilian femora, are *Saltasaurus loricatus Titanosaurus robustus* and *Opisthocoelicaudia skarzynskii*.

The femur of *Opisthocoelicaudia skarzynskii* (holotype ZPAL MgD-I/48) resembles morphotype 2 femur MCT 1692-R in being rather robust. It bears some distinct features, however. In distal view, it shows a strongly developed, anteriorly protruded tibial (medial) condyle, differing from the less developed and shorter medial condyle of the Peirópolis femora (BORSUK-BIALYNICKA, 1977: fig. 15 d). The fourth trochanter of *Opisthocoelicaudia* is also placed below the midline of the femoral shaft, an unique trait of this species (BORSUK-BIALYNICKA, 1977: fig. 15; McINTOSH, 1990: 388). *Titanosaurus robustus* is represented by two femora of the hypodigm (MLP/CS 1125 and MLP/CS 1480). They are very robust, especially in the proximal part of the shafts, in the region of the medial deflection. (HUENE, 1929: lam. 19, fig. 3 and lam. 20, fig. 1). They are a bit constricted near the distal end, differing from MCT 1692-R. *Saltasaurus loricatus* (hypodigm PVL 4017-79) has a robust femur (POWELL, 1992: fig. 37) which, of the three species above mentioned, is the most similar to femur MCT 1592-R of Brazil.

Characters of the femur described in previous Sauropod phylogenies:

The sauropod femur bears some diagnostic features, which have been described in previous works as follows:

SALGADO *et al.* (1997a) have defined three characters concerning the sauropod femur: shape of the shaft in lateral view (n° 4); absence of anterior trochanter (n° 6) and presence of a prominent lateral bulge below greater trochanter (n° 19).

The first character – shape of the shaft in lateral view – may assume two states. The femur may be either sigmoid (primitive state) or straight (the derived condition) in lateral view. According to those authors, the primitive condition is present in theropods and sauropodomorphs, whose femur assumes a rather sigmoid profile in lateral view. In the whole Sauropoda, however, the femur has assumed a straight profile, lacking the typical curvature present in the outgroup femora (SALGADO *et al.*, 1997a: 6).

This character is present in all femora from Peirópolis, attesting their allocation within the Sauropoda.

The second character discussed by SALGADO *et al.* concerns the presence or absence of an anterior trochanter of femur. The primitive retention of this structure within the Sauropoda is exclusive of *Vulcanodon karibaensis*, separating it from all other sauropods (the Eusauropoda clade), which display the derived condition (absence of the anterior trochanter) (SALGADO *et al.* 1997a: 7). The femora from Peirópolis also lack the anterior trochanter.

A third character concerns the morphology of the proximal third of the femur. According to SALGADO *et al.* (1997a: 16), a prominent lateral bulge is present below the greater trochanter of the femur in all Titanosauriformes (a clade comprising *Brachiosaurus brancai*, *Chubutisaurus insignis* and the Titanosauria), being absent in all remaining sauropods.

Other authors also used this character. WILSON & SERENO (1998 – character n° 100), defined it as "femur with proximal one-third of the shaft deflected medially" (WILSON & SERENO, 1998: 52), while SANZ *et al.* (1999 – character n° 40) defined it as "presence of lateroproximal buttress of femur". They also pointed out that this structure is specially developed in some genera as *Saltasaurus* and *Argyrosaurus*, (SANZ *et al.*, 1999: 248).

The character is also present in all femora from Peirópolis, allowing their identification at least within the Titanosauriformes level.

WILSON & SERENO (1998) defined two more characters for the sauropod femur: cross-sectional shape (n° 10) and development of the fourth trochanter (n° 11).

According to those authors, the femur of all sauropods have the derived condition, that is, the femoral shaft has elliptical cross-section, with the long axis oriented mediolaterally. The primitive condition, in which the femoral midshaft is suboval in cross-section is present both in theropods and prosauropods (WILSON & SERENO, 1998: 28).

The second character discussed by those authors concerns the development of the fourth trochanter of femur (character n° 11 of their analysis). According to them, the fourth trochanter in prosauropods and theropods projects from the shaft as a distinct flange with a characteristic subrectangular profile among prosauropods and a crescentic profile among theropods. In sauropods, however, the fourth trochanter is reduced to a low crest (WILSON & SERENO, 1998: 28). The reduction of the fourth trochanter in sauropods may be related to their obligatory quadrupedal posture and large body size (WILSON & SERENO, 1998: 29).

This character was also used by SANZ *et al.* (1999 – character n° 41 of their analysis).

The two characters are also present in the Peirópolis femora. Unfortunately, these characters are synapomorphic for the Sauropoda, and thus are not useful to clarify the relationships within the Titanosauridae.

TIBIA

The posterior limb is composed by two epipodials, the tibia and fibula. The tibia is long and medially placed, being always stouter than the fibula in reptiles. (ROMER, 1956: 374). In theropod and ornithopod dinosaurs, the tibia bears a prominent, well developed cnemial crest, which is comparatively less developed in sauropods (ROMER, 1956).

In sauropods, the tibia is straight and has an expanded proximal end, on the lateral face of which is a strong cnemial crest, that cradles the proximal end of the fibula (McINTOSH, 1990: 372). The cnemial crest is the point of insertion of some important muscles of the hind limb: the *ambiens* (amb), the *iliotibialis* (il tib) and the *iliofemoralis* (il fem) (BORSUK-BIALYNICKA, 1977: fig. 16 b) (Fig. 10).

The tibial shaft is slightly flattened anteroposteriorly and its anterior surface bears the insertion points for the *tibialis anterior* (ta), and the *peroneus longus* (perl) (BORSUK-BIALYNICKA, 1977: fig. 16 b). The distal end of the tibia is less expanded than the proximal one. A process that locks the astragalus in place is found on the posteromedial

side of the distal end of the tibia (McINTOSH, 1990: 372). The posterior margin of the tibia head receives the *flexor tibialis* (flt), which comes from the ilium and the ischium; and the *gastrocnemius* (gast), which is responsible for the extension of the foot (BORSUK-BIALYNICKA, 1977: fig. 17 b).

The tibia is shorter than the femur, and the two bones vary their relative proportions within the Sauropoda. In Diplodocids, the tibia:femur ratio is 0.65 to 0.69 in *Diplodocus* (McINTOSH, 1990:389) and 0.60 in *Apatosaurus* (McINTOSH, 1990: 390). This ratio is 0.62 in the Dicraeosaurinae *Dicraeosaurus* (McINTOSH, 1990: 393). In *Camarasaurus* (representing the Camarasauridae) the tibia:femur ratio is greater than that of brachiosaurids, but less than that of diplodocids. The lowest value is found in *Brachiosaurus* (Brachiosauridae), whose tibia:femur ratio is 0.58. The tibia in this genus is massive, and bears a well-developed cnemial crest (McINTOSH, 1990: 382).

In the Titanosauridae, the tibia:femur ratios turn out to be higher, reaching values similar to those found in diplodocids. They range from 0.65 in *Titanosaurus indicus* and 0.67 in *Antarctosaurus wichmannianus* to 0.69 in *Aegyptosaurus* (McINTOSH, 1990: 395 and 397).

General observations:

There are four tibiae within the material under study (Tables 35 and 36, Fig. 20). Two are large (MCT 1683-R and MCT 1695-R), and two are small (MCT 1587-R and MCT1681-R).

Two of them (MCT 1587-R and MCT 1695-R) have come from "Serra da Galga" deposits. MCT 1587-R is a small tibia. It is broken in the middle and has lost part of the shaft, but it is well preserved. The other tibia (MCT 1695-R) is two times longer and has been associated to "Serra da Galga" (*fid.* Diógenes Campos). The overall preservational state of the bone, with both ends showing signs of abrasion, seems to confirm this provenance.

The other two remaining tibiae (MCT 1681-R and MCT 1683-R) are from uncertain provenance, so they have been scored as "Peirópolis surroundings". MCT 1681-R (right) is small, the same size of MCT 1587-R, and is very well preserved. MCT 1683-R (right) is a large tibia, and part of its cnemial crest is broken off. The bone is in good state of preservation, however.

Morphology:

The tibiae from Peirópolis have a straight shaft with both ends expanded (Fig. 42). The superior extremity bears a well developed cnemial crest (cn cr), and the distal end is more transversally than anteroposteriorly expanded, a typical trait found in the Titanosauria (SALGADO *et al.*, 1997a: 8) (Fig. 42 – B).

In lateral view, the tibia exhibits a stout, wide shaft, with a straight posterior margin and a concave and curved anterior one. The tibial head is well developed, being more of less rectangular in shape, with both anterior and posterior upper corners projecting themselves outside the rectangle. The surface of this area bears a small concavity (cnc) in its middle (Fig. 42 – A). The anterior border of the tibial head plunges steeply to meet the base of the cnemial crest. The cnemial crest rises from the anterior medial corner of the tibial head, and is rather triangular in shape. It points forward, and is a bit laterally twisted. The base of the triangle splays itself over the anterior margin of the tibia, covering the upper third of the bone. The lateral surface of the cnemial crest is crossed by a shallow digitiform depression, which comes from its upper border and descends vertically, covering a variable distance among the different tibiae (Fig. 42 – F - dgt). The distal portion of the tibia is less expanded than the head, and is subdivided in two condyles, one anterior and one posterior. The anterior condyle (ant cnd) is the articular area for the ascending process of the astragalus. The other, the posteroventral condyle (pos cnd), is the less developed of the two condyles, and its lower surface is set at a plane below that of the anterior condyle (Fig. 42 – A).

In anterior view, the tibia reveals a narrow, mediolaterally compressed shaft, with concave lateral and medial margins, and both ends expanded (Fig. 42 – B). In this view, however, the distal end is wider than the proximal one. The anterior lobe of the cnemial crest is a little flattened, probably for the attachment of the muscles *ambiens*, *iliotibialis*, and *iliofemoralis*. The anterior distal condyle is well developed and laterally projected, contributing for the enlargement of the transversal dimension of the distal end.

In medial view the tibia shows the same silhouette as in lateral view. It is totally flattened, unless for the presence of a medial elevation, placed near the posterior margin of the tibial head (Fig. 42 – C - med el).

In proximal view the tibia has a almost quadrangular shape, being little longer than wide. The lateral border is rather straight, while the medial border is slightly convex. The cnemial crest is visible protruding from the anterior medial corner of the tibial head (Fig. 42 – D). The proximal surface of the tibia is slightly concave over almost all its area, with a convex elevation at the anterior border, placed just where the cnemial crest begins. This surface is covered by bumps, rugosities and deep grooves, mainly in the lateral and posterior margins.

In distal view, the tibia assumes a rather elliptical shape, but the anterior margin of the ellipse is broken by the presence of the two distal condyles. The anterior condyle is the most developed, projecting itself beyond the limits of the ellipse. The posterior condyle is blunt, and restricted to the elliptical shape of the distal end. Between the two condyles lays a deep and well developed notch (Fig. 42 – E – nt).

The four tibiae are very alike in the morphology displayed, and we were not able to establish differences that could justify their segregation in different morphotypes. There are some individual features, however, that have been discussed below.

Material: MCT 1587-R, MCT 1681-R, MCT 1683-R and MCT 1695-R.

MCT 1587 (left) (Fig. 42 – F; Fig. 106): this tibia is broken in two parts, and has lost some of its middle. It is also mediolaterally crushed, which makes the proximal end too contorted. Nevertheless, it is not different from the general pattern displayed by other tibiae from Peirópolis. MCT 1587-R shares with MCT 1681-R the same general proportions, and may be paired with it. The digitiform depression is present over the lateral surface of the cnemial crest. It is about 10 cm long, being longer than in MCT 1681-R (Fig. 42 – F). The lateral surface of the tibial head bears a small, oval elevation, instead of the concavity found in MCT 1681-R and other tibiae.

MCT 1681 (right) (Fig. 42 – A to E; Fig. 107; Fig. 108): this tibia was the base for the general description included in the beginning of this morphology section, so, there is not much to add here. The digitiform depression on the cnemial crest is about 6 cm long.

MCT 1683-R (right) (Fig. 109): this is one of the largest tibiae present within the Peirópolis material. This tibia shows the same general morphology of other tibiae. The lateral surface of the tibial head is concave as in MCT 1681-R. It differs from this tibia, however, by some features of the distal end. In MCT 1683-R, both distal condyles are

extremely well developed, ant the anterior one is slender and more tapered than the posterior one, whereas, in the smaller tibia, the anterior condyle is the widest. The distal end of MCT 1683-R assumes also a more elliptical outline, with a curved, convex anterior margin, whereas in MCT 1681-R this margin is straight. Due to the incompleteness of the cnemial crest, the presence of a digitiform depression on it cannot be confirmed.

MCT 1695-R (right) (Fig. 110): is almost the same size of MCT 1683-R. It displays the normal morphology of all other tibiae from Peirópolis, but the shape and the relative development of the distal condyles cannot be evaluated, since they have been eroded away. The lateral surface of the tibial head bears a concavity, but it is displaced down the shaft. The cnemial crest is strongly beveled laterally, and the digitiform depression is present, but is comparatively shorter than in MCT 1587-R.

Comparisons within bones:

The tibia from Peirópolis exhibit a rather uniform morphological pattern, and we were not able to detect within the material any morphological differences that could justify their separation in different morphotypes. The few differences existing among the bones (as the presence of a concavity over the lateral surface of the tibial head, or the relative development of the distal condyles) are here considered as mere results of normal variation or size development. As for the humeri, it is possible that either the tibiae of the Peirópolis sauropods showed the same morphology, or tibiae of different morphotypes have been not preserved in the sample. More material is necessary to confirm or dismiss these hypothesis.

Comparisons with other taxa:

The Peirópolis tibiae have been compared with the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Antarctosaurus wichmannianus*; *Argentinosaurus huinculensis*; *Chubutisaurus insignis*; *Laplatasaurus araukanicus*; *Laplatasaurus sp.* (=*Antarctosaurus sp.*); *Gondwanatitan faustoi*; *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Saltasaurus loricatus*; *Titanosaurus australis* (=*Neuquensaurus australis*) and *Titanosaurus robustus* (=*Neuquensaurus robustus*).

The right tibia of *Argentinosaurus huinculensis* (PVPH-1 – holotype), although incomplete, is the most slender tibia found among titanosaurians, being easily distinguished from the tibiae of Peirópolis by its non triangular, poorly developed cnemial crest (BONAPARTE & CORIA, 1993: fig. 8). The identification of the tibia of *Argentinosaurus* was questioned by WILSON & SERENO (1998: 43), who considered the bone to be a fibula. The figured tibia of *Argentinosaurus* resembles a fibula in medial view. If it is a fibula, than it is very similar to MCT 1696-R from Peirópolis, whose shaft and fibular crest are so developed, that the bone can be easily misidentified as a tibia.

The tibiae of *Opisthocoelicaudia skarzynskii* (holotype) are stout bones, which differ from Peirópolis tibiae by having more straight shafts in anterior view (BORSUK-BIALYNICKA, 1977: fig. 16 b). The upper border of the cnemial crest in *O. skarzynskii* seems to be placed well below the upper margin of the tibial head (BORSUK-BIALYNICKA, 1977: pl. 11, fig. 4; pl. 14, fig. 2). In the Brazilian bones, the crest begins adjacent to the upper margin of the tibial head.

The tibia of *Lirainosaurus astibiae* (MCNA 7471 – paratype) resembles the Brazilian tibiae, but may be promptly distinguished from them by the slenderness of its shaft (SANZ *et al.*, 1999: pl. 6 b). In fact, the Spanish species seems to have the most slender tibiae of all known titanosaurids. A similarity lays on the angle between planes including the greatest proximal and distal dimensions. This angle is low in the Peirópolis material (at about 50°), as well as in the Spanish species (SANZ *et al.*, 1999: fig. 3 and character/taxon data matrix). In this respect, they both differ from the strongly twisted shaft of *Saltasaurus*, whose greatest proximal and distal dimensions are set in almost perpendicular planes (SANZ *et al.*, 1999: fig. 3, and character/taxon data matrix).

The right tibia of a juvenile *Saltasaurus loricatus* (PVL 4017-87), is similar in overall shape to the tibiae from Peirópolis (POWELL, 1992: fig. 39). The right tibia assigned to an adult form (PVL 4017-84 – hypodigm), differs from the Brazilian tibiae by some aspects, however (POWELL, 1992: fig. 38). It is more robust, especially in the head, which is very broad in lateral view. In anterior view, the distal end of the bone is extremely developed, showing expanded lateral and medial borders. The cnemial crest is strongly twisted to the lateral side, and its superior margin seems to bear a reentrance, with the portion closer to apex of the triangular cnemial crest being thickened. The shape of the distal end was not figured either, hindering further comparisons.

The hypodigm of *Titanosaurus australis* is represented by three tibiae. The left tibiae (MLP/CS 1103) differs from the Brazilian bones by having a more developed cnemial crest, with a strong anteriorly projected orientation, so that the bone, in lateral view, is much broader proximally than distally (HUENE, 1929: lam 16, fig. 2). The distal end of an incomplete right tibia (MLP/CS 1093) has a heart-shaped profile, and the two distal condyles seem to be equally developed (HUENE, 1929: lam. 16, fig. 4). As *Titanosaurus australis*, the left tibia of *Titanosaurus robustus* (MLP/CS 2064 – hypodigm) also differs from the Brazilian material by possessing a well developed and anteriorly directed cnemial crest and a broad expanded distal end. The shaft is also stout and broader than in the Brazilian tibiae, which are comparatively slender (HUENE, 1929: lam. 19, figs. 4 a-b) . The distal end, however is similar to Peirópolis tibiae, with a anterior condyle more developed than the posterior one (HUENE, 1929: lam. 19, fig. 4 d).

The presence of a digitiform depression on the cnemial crest cannot be confirmed in any of the taxa above discussed.

There are some taxa whose tibiae bear similarities with the Brazilian tibiae, and nevertheless, can be also distinguished from them. Among them are *Antarctosaurus wichmannianus*, *Chubutisaurus insignis*, *Aelosaurus sp.* and *Laplatasaurus araukanicus*.

We have examined the left tibiae of both *Antarctosaurus wichmannianus* (MACN 6904 – holotype) and *Chubutisaurus insignis* (MACN 18222 - holotype) during a visit to the MACN (Buenos Aires, Argentina). The tibiae of these species are similar to the Peirópolis tibiae in overall shape. The cnemial crests show similar development. The tibial head is transversally expanded, and its lateral border is slightly concave, a trait also present in the largest Brazilian tibiae. *Antarctosaurus wichmannianus* differs from the Brazilian material by the more circular profile displayed by the distal end, contrasting with the more elliptical profile of the Brazilian tibiae. The cnemial crest is not laterally twisted in the Argentinean species, making a right angle with the tibial head, and the digitiform depression is absent. The cnemial crest of *C. insignis* bears a digitiform depression, but it is divided in two parts by a low, transverse elevation, differing from the Brazilian material.

The left tibia of *Aelosaurus sp.* (MPCA-27100) is similar to the tibiae from Peirópolis in overall shape (SALGADO, CORIA & CALVO, 1997b: fig. 5b). The shaft is equally slender, and the cnemial crest, although a bit longer, is also a little laterally twisted (the presence of a digitiform depression is uncertain). The tibial head is almost quadrangular in proximal view, and its lateral border bears a concave curve, similar to that

found MCT 1683-R. The tibia of the holotype of *Aelosaurus rionegrinus* (MJG-R1) was neither figured, nor described in the original work (POWELL, 1987b), hindering further comparisons. If the tibiae of *A. rionegrinus* and *Aelosaurus sp.* are similar to each other, than the former might be equally similar to tibiae from Peirópolis.

The tibiae attributed to *Laplatasaurus araukanicus* (MLP/CS 1128 and MLP/Av. 2062) show the greatest similarities with the tibiae from Peirópolis. They have a similar slender shaft, with a concave tibial head that bears an equally developed, laterally twisted cnemial crest (HUENE, 1929: lam. 27, figs. 1 and 3). The distal end is also elliptical, and the distal condyles show a similar pattern of development, with the anterior condyle being the longer of the two (HUENE, 1929: lam. 27, fig. 4b). The presence of a digitiform depression on the cnemial crest cannot be confirmed by the available figures. Unless it is crushed, the right tibia of *L. araukanicus* (MLP/CS 1128) seems to be more anteroposteriorly elongated than the tibiae from Peirópolis (HUENE, 1929: lam. 27, fig. 1c). The cnemial crest seems to have a longitudinal ridge running along its medial surface (HUENE, 1929: lam. 27, fig. 1b). A similar feature was reported the additional specimen identified as *Laplatasaurus sp.* (POWELL, 1979: 198). This ridge, although incipient, is also observable in MCT 1681-R and MCT 1695-R. The right tibia of *Laplatasaurus sp.* (PVL-3670-5 - holotype), although incomplete and damaged, has some morphological traits in common with the Peirópolis material: in lateral view, its posterior margin is straight, and the anterior one is concave; and the axis of the shaft is arched, with the concavity laterally oriented (POWELL, 1979: 197).

The last taxon to be considered is *Gondwanatitan faustoi*, which is the only Brazilian sauropod whose tibia is known. The left tibia of *Gondwanatitan faustoi* (MN 4111-V – holotype), is very similar to the other tibiae from Peirópolis, specially the smallest ones. The anterior margin of the proximal articulation is the highest point of the tibia in lateral view (KELLNER & AZEVEDO, 1999: 136). This trait is also present in the tibiae from Peirópolis. The lateral surface of the tibial head is also a little concave. The lateral surface of the cnemial crest bears a long digitiform excavation similar to that present in MCT 1587-R. This is a further indication that *G. faustoi* must be represented among the fossil remains of Peirópolis.

Characters of the tibia described in previous Sauropod phylogenies:

There are several characters described for the tibia in previous sauropod phylogenetic studies.

WILSON & SERENO (1998) have defined three characters for the tibia: orientation of the cnemial crest (character n° 47); size of the distal posteroventral process of the tibia (n°48), and shape of the proximal condyle (character n° 83).

The first character (n° 47) concerns the orientation of the cnemial crest of the tibia, and has two states: it may be either anteriorly oriented (the primitive condition) or laterally oriented (the derived condition). According to those authors, the anteriorly oriented cnemial crest is present in prosauropod, basal theropods and the sauropod *Vulcanodon* (WILSON & SERENO, 1998: 40). In Eusauropods, the cnemial crest displays the derived state, that is, it is the cnemial crest is directed laterally as a thin plate-shaped flange, partially obscuring the proximal end of the fibula in anterior view (WILSON & SERENO, 1998: 40).

The derived condition is present also in the tibia from Peirópolis, which have laterally twisted cnemial crests.

The second character discussed by WILSON & SERENO (1998: character n° 48) concerns the development of the posteroventral process of the tibia. This process may be ether broad transversely, covering the posterior fossa of astragalus (the primitive condition) or reduced, making the posterior fossa of astragalus visible posteriorly (the derived condition).

According to WILSON & SERENO (1998: 40), the primitive condition is present in prosauropods and theropods, where the posteroventral process of the tibia extends laterally toward the calcaneum, completely obscuring the posterior fossa of the astragalus in posterior view. In *Vulcanodon*, the condition is unknown, but is all eusauropods, the posteroventral process does not extend laterally to approach the calcaneum. As a result, the posterior fossa of the astragalus is exposed in posterior view (WILSON & SERENO, 1998: 40). This trait is also present in the tibia from Peirópolis.

The third and last character discussed by those authors concerns the shape of the proximal condyle of the tibia (n° 83), which may be ether narrow, with an anteroposterior long axis (the primitive condition) or expanded transversely, with a subcircular proximal end (the derived condition).

According to WILSON & SERENO (1998: 48), the transverse dimension of the proximal end of the tibia is always less than its anteroposterior dimension (the former measuring approximately 55% to 75% of the latter) in prosauropods, theropods, and the sauropods *Vulcanodon* and *Barapasaurus*.

In neosauropods, the proximal end of the tibia is subcircular with subequal anteroposterior and transverse dimensions (WILSON & SERENO, 1998: 48).

The tibiae from Peirópolis display the derived condition, being even rather quadrangular in proximal view.

SALGADO, CORIA & CALVO (1997a) defined only on character for the tibia: proportion of the distal end of the tibia (character n° 7 of their analysis).

This character may display to states: the distal end of the tibia may be either more transversely than anteroposteriorly expanded (the primitive condition), or the anteroposterior diameter is subequal/greater than distal width (the derived condition)

According to those authors, the primitive condition is present in prosauropods and presumably in the basal sauropod *Vulcanodon* (SALGADO *et al.* 1997a: 8). In Eusauropoda (a clade comprising all sauropods except *Vulcanodon*) the distal end of the tibia is expanded, at least, as much anteroposteriorly as it is transversely so (the derived condition), being regarded as a synapomorphy of sauropods more derived than *Vulcanodon karibaensis* (SALGADO *et al.*, 1997a: 8).

Sauropods of their Unnamed taxon I (*Chubutisaurus insignis* + Titanosauria), however, have the plesiomorphic condition, and have reverted to the primitive condition for dinosaurs (distal end of tibia more transversely than anteroposteriorly expanded) (SALGADO *et al.* 1997a: 8).

The tibiae from Peirópolis have also distal ends more transversely than anteroposteriorly expanded, and may be allocated within the Unnamed Taxon I of SALGADO *et al.* (1997a).

SANZ *et al.* (1999) went further and refined this trait of the Titanosauria in their character n° 42, angle between planes including the greatest proximal dimension of the tibia and that of the distal region, which may be either low (the primitive condition) or almost perpendicular (the derived one).

According to those authors, among the Titanosauria the derived condition is present only in *Saltasaurus*, while *Epachthosaurus* and *Lirainosaurus* bear the primitive condition, and, in *Argyrosaurus* and the "Peirópolis titanosaur", the character is unknown (SANZ *et al.* 1999: 248 – character taxon data matrix).

This angle in the Peirópolis tibiae stands between 50° and 55° (MCT 1681-R). This may be not "low", but, nevertheless, it is not the perpendicular state found in the high derived *Saltasaurus*.

FIBULA

The fibula is one of the two epipodials of the posterior limb. It is expanded at both ends and markedly concave toward the tibia (ROMER: 1956: 374). In archosaurians the tibia and fibula are generally long and relatively slender elements, with the fibula reduced to a degree somewhat comparable to that found in mammals. (ROMER, 1956: 376).

In sauropods, the fibula has a straight shaft, and it is as long as or longer than the tibia (CHRISTIANSEN, 1997: 321). The proximal end is flattened, and on its medial side there is a triangular muscle scar (McINTOSH, 1990: 373). On the external face of the shaft, and placed about the middle of it, the fibula shows another prominent muscle scar, that serves as the point of insertion of the muscle *flexor digitorum longus* (fdl) (BORSUK-BIALYNICKA, 1977: 41 and fig. 17) (Fig. 10). The *iliofibularis* (il fib) is another important muscle that comes from the posterior process of the ilium and inserts into a flattened rugose area on the posterior margin of the proximal portion of the fibula (BORSUK-BIALYNICKA, 1977: fig. 17 b), helping the flexion of the crus (Fig. 10). The medial face of the distal end of the fibula is convex where it roughly abuts into a concavity on the lateral face of the astragalus (McINTOSH, 1990: 373).

There is no much information about the comparative morphology of the fibula among sauropods. The muscle scar on the lateral face of the fibula is weak in the primitive *Shunosaurus* (Cetiosauridae) (McINTOSH, 1990: 379). In *Brachiosaurus* the fibula is barely longer than the tibia, and massive, with little development of the muscle scar on its lateral face. The inwardly directed process on the distal end, which fits loosely into the lateral concavity of the astragalus, is unusually large (McINTOSH, 1990: 382). In diplodocids (e.g. *Diplodocus* and *Barosaurus*) the fibula is usually slender, differing from the more robust shape found among the Titanosauridae.

General observations:

Six fibulae compose the material from Peirópolis (Tables 37 and 38, Fig. 21). The provenance of all of them is known. There are two fibulae from each one of the three main collecting sites. The fibulae vary in shape and size (Fig. 114 – D to G).

The two left fibulae from "Serra da Galga" are the smallest (MCT 1588-R) and the largest (MCT 1696-R) of all bones. They are indicative that the "Galga" sample is formed

by a mixture of both small (maybe young) and larger (maybe adult) individuals. These two bones are in very good state of preservation, showing minute morphological details.

There are also two fibulae from the "Rodovia" site (MCT 1607-R and MCT 1608-R). Both are right fibulae, which shows that the material of this site does not belong to a single individual. They are intermediate in size between the previous two bones. They are robust, and display the same morphology. MCT 1608-R is complete, shows good estate of preservation, bearing few erosion marks. MCT 1607-R is broken, and lacks the distal third, but it is still in good state of preservation. This fibula is just a little smaller than MCT 1608-R.

The last two fibulae from Peirópolis (MCT 1657-R – left, and MCT 1660-R - right) were unearthed at "Site 1" at the same year (1959). They are the same size, forming a perfect pair, which suggests that they could have belonged to the same individual. They show minute differences in the morphology of their lateral tuberosities, however, which will be discussed below. MCT 1660-R displays a better state of preservation than MCT 1657-R, which is a little eroded at both proximal and distal ends. These two bones are a little longer than MCT 1588-R.

Morphology:

The fibulae from Peirópolis show the normal morphology presented by titanosaurid fibulae in general (Fig. 43 and 44). It is difficult to find distinct diagnostic morphological traits that could differentiate them from each other or from other species of titanosaurids.

In lateral view, the fibula shows a straight shaft, with both ends expanded, the proximal one a bit more than the distal. The lateral surface is convex throughout its length. The anterior border of the shaft is a little concave, unless in its upper quarter, where it is rather straight. This difference lays on the presence of a crest, which projects itself anteriorly. The posterior border of the shaft follows a weak concave curve. The shaft is constricted at about midlength. The breadth of the shaft at this point varies within the morphotypes identified (see below). Just above the transverse midline, the fibula bears a distinct swelling, which protrudes from the surface of the shaft outwards, forming a lateral tuberosity or lateral trochanter (Fig. 43 – A, B; Fig. 44 – C, D – lat trc). The swelling is set obliquely over the lateral surface of the shaft, the upper portion near the anterior border, ant the lower portion adjacent to the posterior border, even contributing to form its margin.

This tuberosity is typical of all sauropods, except *Vulcanodon* (WILSNO & SERENO, 1998: 40), and may have been the insertion zone of the muscle *flexor digitorum longus* (BORSUK-BIALYNICKA, 1977: 41 and fig. 16 a). The tuberosity is rugose, and shows some morphological variation (see below). At the frontal area of the upper, anterior portion of this swelling, there is an anterior protuberance, which may be the anterior trochanter (ant trc) (WILSON & SERENO, 1998: 40 – see section 11.7). It is well marked in some fibulae, and absent in others (Fig. 44 – A). The proximal portion of the fibula, just above the swelling, may be subdivided in anterior and posterior parts. The posterior part looks like a cylindrical stalk (st), being wide and stout, strongly convex, and continuous with the shaft (Fig. 43 – B; Fig. 44 – A - st). It lays a bit inclined to the posterior direction, and its upper margin is a bit convex, and marginated by longitudinal grooves. The anterior portion of the fibula is very reduced in relation to the other. In fact, it is a laminar expansion of the latter, which projects itself forwards and inwards as a fibular crest (fib cr) (Fig. 43 – B, C, D; Fig. 44 – A, B, E). It is shaped as a inverted triangle, and its upper margin is downwardly inclined. Its lateral surface forms a concavity limited posteriorly by the anterior margin of the fibular stalk. This structure is very reminiscent of the cnemial crest of the tibia, especially in MCT 1696-R (the largest fibula). The distal end of the fibula is expanded in anteroposteriorly direction. The lower margin is bordered by longitudinal grooves, and bears an elevation, outward projected, which varies in development among the different fibulae.

In medial view the fibula keeps the same outline, but the medial surface is flat over the middle of the shaft to slightly concave over the distal portion. There is no special muscle scar visible on the medial surface, unless that for the articulation with the tibia. The proximal portion of the fibula is still divided into an anterior crest and a posterior stalk, but here, none of this structures seems to prevail over the other, contributing equally to the constitution of the fibular head. The crest is almost coplanar with the stalk, and the pair forms a concave surface. This surface corresponds to the tibial articular surface(tb art). It is covered by small longitudinal striae, and its triangular shape is not at all distinct (Fig. 43 – D; Fig. 44 – E). In some fibulae, a rugose oblique ridge (obl rdg) arises abruptly from the middle of the surface, separating the two structures (Fig. 44 – B, C, E). This ridge begins on the upper margin of the fibular head and descends obliquely in anterior direction, merging with the bone surface after a short distance. The distal end of the fibula displays a shallow depressed surface, which is marginated anteriorly and posteriorly by slightly

thickening of both anterior and posterior distal borders; and inferiorly, by the rugose rim of the margin of the distal end.

In anterior view, the shafts of the fibulae assume a contorted shape, being medially deflected in the upper third, beginning the deflection in the point where the lateral tuberosity is placed. The stalk, nevertheless, stays straight, being visible in part beyond the fibular crest. The fibular crest points a little medially, and its surface is rugose. The anterior trochanter, when present, may be perceived as a small elevation in this perspective. The lateral trochanter, however, is well visible as a triangular protuberance arising from the lateral margin. Below the upper third, the shaft of the fibula is straight. The anterior border may be highlighted, in the larger bones, by the presence of a longitudinal ridge, which is the continuation of the anterior margin of the fibular crest. This ridge descends along the mid portion of the shaft, and then, at the lower third, it roughens and makes a curve, which is concave to the lateral side. The distal end is straight medially, and the lateral margin bears a protuberant expansion, which points outward.

In posterior view, the fibular outlook is not so different from the anterior view. At this perspective, however, the upper stalk of the fibular head is better viewed. The stalk is wide up and tapers gradually down, assuming the shape of an inverted cone. The apex of the inverted cone merges into the shaft near its medial border, at the same plane where the lateral trochanter arises from the bone. The space between these two structures is filled by a concave depression. The upper margin of the conic stalk is flattened. Beyond it, it is possible to see part of the inner surface of the fibular crest. When present, the medial oblique ridge that separates crest from stalk is clearly seen as a medially pointing, rugose tuberosity. The posterior margin of the fibula is not highlighted by a longitudinal ridge.

In proximal view, the fibular head displays an elliptical outline, with a flap-like structure which correspond, respectively, to the stalk and the fibular crest. The proximal surface of the stalk is longer anteroposteriorly than wide. The fibular crest projects itself from the anterior medial corner of the head, pointing obliquely forwards and inwards. The medial margin of the fibular head is subdivided, thus, in a concave surface (the crest), immediately followed by a convex surface (the stalk). This sinuous curvature is only broken by the occasional presence of the medial oblique ridge, signaled by a small medial elevation. The distal surface is rugose and crossed by grooves.

In distal view, the fibula displays a "D" shaped outline, with the bar of the "D" corresponding to the medial margin (Fig. 43 – E; Fig. 44 – F). The "D" shaped distal end is

a little asymmetrical, the anterior border being somewhat straight, the posterior one being more pointed. The distal surface is rugose and all covered by grooves, but over the posterior half, these markings are more conspicuous than over the anterior half.

The fibulae from Peirópolis fall in one of either two recognized morphotypes.

Morphotype 1:

Material: MCT 1588-R, MCT 1657-R and MCT 1660-R

Description: morphotype 1 is identified by the slenderness of the shaft, and displays the basic morphology found in the Peirópolis fibulae in general, as described above (Fig. 43). This category, in fact, is characterized by the absence of a set of features that are proper of morphotype 2. The most important characters of morphotype 1 are, thus, absence of a well developed anterior trochanter on the anterior margin of the shaft; and absence, in the fibula head, of a medial oblique ridge between the stalk and the fibular crest.

Nevertheless, the morphotype 1 category bears some characters of is own, such as the slenderness of the shaft, proportionally much more constricted in the middle than in morphotype 2; and the shape of the proximal distal end, which is more flattened mediolaterally than in morphotype 2 fibulae.

The lateral trochanter in morphotype 1 show some variation, being divided or undivided. This trait will be better described below.

MCT 1588-R (left) (Fig. 111): this fibula is the smallest of all. The lateral trochanter is oval and non-divided. In medial view, the stalk is well distinct from the fibular crest, but there is no medial oblique ridges separating them. The lower medial surface is not so concave as in other fibulae. In proximal view, the bone displays an elliptical profile, with the anteroposterior axis being almost two times longer than the mediolateral width. In distal view, the bone shows a "D" shape profile, the bar corresponding to the medial margin, which is marked by grooves.

MCT 1657-R (left) (Fig. 117) MCT 1660-R (right) (Fig. 43; Fig. 115; Fig. 116): these two bones display the normal morphotype 1 category. They are slender fibulae, whose shafts are well constricted in the middle. The most interesting feature displayed by these fibulae concerns the shape of the lateral trochanter. This trochanter is normally a

rounded to oval structure, marked by an ample rugose scar. In these two fibulae, however, this pattern shows some variation. The scar becomes divided. This condition is incipient in MCT 1657-R, but well developed in MCT 1660. In the latter, the divided scar forms even two longitudinal conspicuous ridges, which run parallel to each other.

Morphotype 2

Material: MCT 1607-R, MCT 1608-R and MCT 1696-R

Description: morphotype 2 bones are rather robust, being not so constricted in the middle of the shaft. They are easily recognized by the presence of a well developed anterior trochanter, placed above the medial tuberosity, and anteriorly to it. In medial view, the fibula head shows the oblique medial ridge that divides the head into the stalk and crest. It is well developed, and, in both posterior and proximal views, it is visible as a protuberant structure pointing medially. This ridge is absent in morphotype 1 fibulae (Fig. 44 – obl rdg). In proximal view, the stalk is less mediolaterally flattened, being proportionally wider than morphotype 1 stalks. The fibular crest is well developed, and the medial oblique ridge is visible as a small protuberance over the internal margin of the fibular head (Fig. 44 – E). The distal ends of morphotype 2 fibulae are also more mediolaterally expanded than in morphotype 1, perhaps a result of the overall increase in bone stoutness (Fig. 44 – F). The lateral trochanter does not show the variation observed in morphotype 1 fibulae.

MCT 1607-R (right) (114 - A) and MCT 1608-R (right) (Fig. 44; Fig. 112; Fig. 113; Fig. 114 – B, C for comparison): the lateral trochanter is well developed, rounded in lateral view, conical in anterior view, and undivided. The anterior trochanter is present, and well developed. It takes form of a curved elevation, which, in frontal view, delimits a concave area with the fibular crest. The anterior margin of the shaft is covered by a longitudinal ridge, which (at least in MCT 1608-R) descends down to the distal anterior margin of the bone. The lower portion of this ridge is very roughened and curved, with the concavity facing outwards.

In medial view, the lower third of MCT 1608-R shows a concave surface. This surface is limited posteriorly by a thickening of the posterior margin, and anteriorly, by the roughened portion of the anterior longitudinal ridge described above.

In proximal view, the fibular head is elliptical, and less anteroposteriorly expanded in relation to its breadth than morphotype 1 fibulae. The fibular crest is present as a well developed, thick structure, and the oblique medial ridge is also visible.

In distal view, the bone is not so "D" shaped, but rather sub-circular in profile. Its medial margin seems to bear a kind of notch in the mid-line, but, because this extremity is the most eroded part of the bone, and MCT 1607-R, although better preserved, lacks the distal end, it is not sure whether this trait is natural or a artifact of preservation.

MCT 1696-R (left) (Fig. 118): is the largest of all fibulae. It shows all the attributes of a typical morphotype 2 fibula: the anterior trochanter is present. The lateral one is oval, rugose, undivided. The fibular crest is extremely developed. The medial aspect of the fibular head bears a medial oblique ridge. The distal medial surface is concave. The most striking feature of this bone is its robustness. The shaft of this fibula shows an increase in the medial-lateral dimension, better realized in proximal and distal views. The breadth of each extremity almost equals the respective width, so that all the bone displays a rather cylindrical shape.

Comparisons within morphotypes:

The presence of two different morphotypes within the Peirópolis material is consistent with all data already assembled, which hints at two well different morphologies for the majority of bone categories studied. The presence of two fibulae (MCT 1608-R and MCT 1696-R) of much different sizes within morphotype 2 category suggests that the typical traits of this morphotype are not result of an increase in size.

Comparisons with other taxa:

The Peirópolis fibulae have been compared with the following taxa: *Aelosaurus rionegrinus*; *Aelosaurus sp.*; *Antarctosaurus wichmannianus*; *Laplatasaurus araukanicus* (=*Titanosaurus araukanicus*); *Laplatasaurus sp.* (=*Antarctosaurus sp.*); *Lirainosaurus astibiae*; *Opisthocoelicaudia skarzynskii*; *Saltasaurus loricatus*; *Titanosaurus australis* (=*Neuquensaurus australis*); *Titanosaurus robustus* (=*Neuquensaurus robustus*).

All Titanosauridae fibulae are very similar to each other, being difficult to find distinct morphological characters at generic level. The fibulae discussed herein seem to follow the same scheme of morphotypes 1 and 2, in being slender or robust like bones. The minute details of each morphotype, however, are difficult to be evaluated in other titanosaurid taxa.

The fibulae of *Antarctosaurus wichmannianus* and *Lirainosaurus astibiae* are incomplete, resulting in limited comparisons. The left incomplete fibula of *Antarctosaurus wichmannianus* (holotype MACN 6904) differs from morphotype 2 lacking an anterior trochanter and by the shape of the lateral trochanter, which is developed as a double-ridged structure (HUENE, 1929: lam. 33, fig. 3). Such structure is present only in MCT 1660-R. The Right incomplete fibula of *Lirainosaurus astibiae* (MCNA 7472 – paratype) is a slender-shafted bone (SANZ et. al. 1999: pl.6 c), similar to morphotype 1 bones. The presence of the typical traits of morphotype 2 cannot be confirmed by the given figure.

Some taxa seem to share some traits with both morphotypes 1 and 2 at the same time. The left fibula of *Saltasaurus loricatus* (PVL 4017-85 - hypodigm), lacks an anterior trochanter and a medial oblique ridge (POWELL, 1992: fig. 40), being thus similar to morphotype 1. The lateral trochanter, however, is not double-ridged as in MCT 1660-R, being more similar to MCT 1588-R. Nevertheless, the fibula of the Argentinean species is more robust, and has a strong concave medial distal surface (POWELL, 1992: 197); approaching, in both respects, the shape of morphotype 2 fibulae. The estimated length of the fibula is 59.8% of total length of the femur (POWELL, 1992: 197), but this character cannot be accessed in the Brazilian material due to its disarticulated condition.

The fibula of *Opisthocoelicaudia skarzynskii* (ZPAL MgD-I/48 – holotype) shows a fibular crest posteriorly directed (BORSUK-BIALYNICKA, 1977: fig. 16), contradicting the orientation of the fibula considered by other authors (e.g. HUENE, 1929). Nevertheless, the skeleton of *Opisthocoelicaudia* has been found in articulated manner, while all other titanosaurid fibulae have been found in disarticulated manner. This leave us two possibilities: 1) BORSUK-BIALYNICKA committed a mistake, and has switched the both right and left fibulae of *Opisthocoelicaudia*; or 2) The fibula of *Opisthocoelicaudia* is in the right place and all other anatomical reconstructions have been mistakenly done. As we cannot solve this problem (which is not the aim of the present work) without examining the material, we will focus only in the morphological comparison between the Mongolian taxon and the Brazilian material.

The fibula of *O. skarzynskii* is a robust element, which differs from morphotype 2 fibulae by lacking an anterior trochanter. The medial oblique ridge seems to have been substituted by a pair of deep ligamentous foveae (BORSUK-BIALYNICKA, 1977: 41), a trait that may be unique to the Mongolian species. The overall shape of the fibula of *Opisthocoelicaudia* is thus reminiscent of morphotype 1 fibulae, but nevertheless, it still may be separated from them by the more robust shaft, and further from MCT 1660 by the absence of a divided lateral trochanter.

The following taxa discussed have shown to be similar either to morphotype 1 or 2.

The right fibula *Aelosaurus rionegrinus* (MJG-R 1 - holotype) was not figured (POWELL, 1987b), hindering any comparison between *A. rionegrinus* and the Brazilian fibulae. The left fibula of an additional specimen – *Aelosaurus sp.* (MPCA 27100) was reported, however (SALGADO, CORIA & CALVO, 1997b: fig. 5c). The fibula of this specimen is similar to the morphotype 1 fibulae from Peirópolis, for it lacks an anterior trochanter (personal observation). The shaft is also of the slender type. The lateral trochanter is undivided (as in MCT 1588-R). The fibula of *Aelosaurus sp.* seems to be wider in the head than the Brazilian ones. All the following taxa differ from *Aelosaurus sp.* in being more similar to morphotype 2 than to morphotype 1.

The right fibula of *Titanosaurus australis* (MLP/CS 1098 – hypodigm) is very similar to the Peirópolis fibulae (HUENE, 1929, lam 16, fig. 5). The lateral tuberosity seems more developed in the Argentinean taxon. An anterior elevation is noticed, which may be the anterior trochanter. Unfortunately, Huene did not provide a medial view of those fibulae, making it impossible to verify the presence of an oblique medial ridge. The proximal view, however, seems to show an incipient ridge (HUENE, 1929: lam. 16, fig. 5c). The left fibula of *Titanosaurus robustus* (MLP/CS 1265 – hypodigm) is as robust as the morphotype 2 fibulae from Peirópolis (HUENE, 1929: lam. 19, fig. 5). The presence of an anterior trochanter is uncertain, and the presence of a medial oblique ridge cannot be confirmed by the given figures (there is no medial view of the bone). The distal aspect of the fibula of *T. robustus* is rather subcircular in outline (HUENE, 1929, lam. 19, fig. 5d), similar to the profile displayed by MCT 1608-R.

The two fibulae attributed to *Laplatasaurus araukanicus* (MLP/CS 1127 and MLP/CS 1023) display the same morphology as morphotype 2 fibulae from Peirópolis, especially MCT 1696-R, which is almost the same size. The bones are robust, and both extremities are expanded in their medio-lateral dimensions (HUENE, 1929: lam 27, fig. 2c

and 2d). The medial oblique ridge is present in both fibulae of *Laplatasaurus*. In MLP/CS 1127 it is visible in posterior view as a protuberant elevation medially directed (HUENE, 1929: lam. 27, fig. 2b). In MLP/CS 1023, it is clearly seen in medial view (HUENE, 1929: fig. 19a). The anterior trochanter is also present, and is more developed in *Laplatasaurus* than in Brazilian forms. It was interpreted as a double muscular insertion for the "*peroneus*" muscle (HUENE, 1929: 62). The additional specimen identified as *Laplatasaurus sp.* is represented by both right and left fibulae (PVL.3670-6/7). They are incomplete, however, and not well preserved, to allow good comparisons with the Brazilian specimens (POWELL, 1979: fig. 5).

Characters of the fibula described in previous Sauropod phylogenies:

There are only two characters of the fibula described in the in previous sauropod phylogenies, both from the work of WILSON & SERENO (1998): presence of a lateral trochanter (character n° 49) and shape of the proximal tibial scar of the fibula (character n° 62).

The first character concerns the presence of an extra lateral trochanter on the lateral face of the fibula, which indicates the derived state of the character.

According to WILSON & SERENO (1998: 40), in theropods, prosauropods and the basal *Vulcanodon*, just one anterior trochanter is present along the anterolateral margin of the shaft of the fibula, located approximately one-third of the distance from the proximal end of the bone. In eusauropods, in contrast, a second additional elliptical rugosity is present on the lateral side of the shaft of the fibula, located just proximal to midshaft, visible as a swelling on the shaft in anterior or posterior views of the fibula.

This character is present in all fibulae from Peirópolis, indicating that the material belonged undoubtedly to the Eusauropoda (a clade comprising all sauropods except *Vulcanodon*), but is not useful in establishing any relationships within the Titanosauria.

The second character discussed by WILSON & SERENO (1998 – character n° 62) concerns the shape of the proximal tibial scar of the fibula. According to those authors, this scar may be either not well marked (the primitive condition – present in Prosauropods and Theropods) or well marked, and deepening anteriorly (the derived condition).

The derived condition is characterized by the articular surface for the tibia being developed as a well defined, rugose, triangular area that occupies the full width of the fibula

near its proximal articular end and deepening proximodistally toward its ventral terminus in the anterior trochanter (WISON & SERENO: 1998: 43). This condition is synapomorphic for all sauropods (including titanosaurs), except the basal *Vulcanodon* and *Shunosaurus*. They have not discarded the possibility that the character may be also present both in *Vulcanodon* and *Shunosaurus* (WILSON & SERENO, 1998: 43).

The fibulae from Peirópolis bear a tibial scar on their medial proximal surfaces, although this is not so strong. They also show variation in the degree of development of the anterior trochanter.

DISCUSSION

MORPHOLOGICAL VARIATION WITHIN THE MATERIAL

The analysis of the bones from Peirópolis has shown morphological variation, summarized in Table 39.

The majority of bone categories studied herein may be separated in at least two distinct morphotypes. This is the case for the scapula, sternal plate, ulna, femur and fibula.

The scapulae have shown further variation, such as the upper expansions on the scapular blades of the largest bones (MCT 1708-R and MCT 1709-R); or the shapes of the scapular plates with a strong indentation in it (MCT 1691-R and MCT 1708-R); and the progressively shorter acromia in successively larger bones. All this morphological variation may be the result of ontogenetic factors related to growth.

The sternal plate, ulna and femur morphotypes are rather well distinct from each other, showing little further variation. The femur morphotypes are distinguished only on a robust/slender basis, which is, however, a feature common feature among sauropod genera (McINTOSH, 1990: 370). The fibula morphotypes are also well distinct from each other, and the sturdier overall shape MCT 1696-R may reflect only the fact that it belonged to a larger, older animal.

Some categories surpassed two morphotypes, reaching from 3 to 4 morphotypes. This is the case for the radius (with 4 defined morphotypes) and the pelvic bones (pubis and ischium), each one with three distinct morphotypes detected.

The radii from Peirópolis were defined both by overall robustness (morphotypes 1 and 2) as well as by morphological characters (morphotypes 3 and 4). Morphotypes 1 and 2 may reflect normal morphological variation or sexual dimorphism within the same

species, rather than the existence of two different species in the sample. A similar situation is found among the remains of the two Argentinean species of *Titanosaurus* (=*Neuquensaurus*); *T. australis* and *T. robustus* which are considered as synonyms (POWELL, 1986; BONAPARTE, 1996: 107). The radii of morphotype 3, however, are different enough in shape to support the hypothesis of a second species coexisting in the Peirópolis material. Nevertheless, the morphotype 3 radii still represent a problem, since only one of them (MCT 1595-R) is found within the Peirópolis material, whereas the other (MCT 1707-R) may have its origin in a quite different place. The radius included in morphotype 4 category (MCT 1673-R) faces the same kind of problem. Although it has been unearthed in Peirópolis, we know that it does not belong to any of the three main sites of Price studied herein. Nevertheless, its overall morphology is similar to those of morphotypes 1 and 2 and may represent variation within the same population.

The pelvic bones (pubis and ischium) were separated in three distinct morphotypes.

Among the pubes, morphotypes 1 and 3 are similar to each other, but well distinct from morphotype 2. This morphotype was found only in "Serra da Galga" deposits. This suggests that perhaps this morphotype represents a different species from the others. The pubes of morphotypes 1 and 3 may represent individual variation similar to a robust/slender model (as for the radius and femur). Differences in the pelvic bones may be also related to sex dimorphism, but this is very difficult to tell.

The morphological variation presented by the ischia matches that found among the pubes. Morphotype 1 and 2 ischia are alike, but both of them differ well from morphotype 3. Differences between morphotypes 1 and 2 may be sex related, while morphotype 3 may represent a different species.

The existence of 3 different morphotypes among the Peirópolis material agrees with the conclusions reached by CAMPOS & KELLNER (1999) in their study of the three pelves from Peirópolis. These authors considered the three pelves morphologically different from each other, considering them as three distinct new species.

The remaining categories (coracoid, humerus and tibia) display the same morphology in all bones studied, and it was not possible to detect different morphotypes among them. The coracoids are very alike, and those that show some morphological variation (MCT 1653-R and specially MCT 1691-R) are also the smallest bones within the category. So, this variation was here considered as the result of growth patterns. Only the discovery of new bones will help to clarify the coracoid question.

The humeri and tibiae are very conservative in their morphologies, displaying almost no individual variation. This is surprisingly unexpected, since both bones are important limb elements, receiving several different muscles from both pectoral and pelvic girdles, respectively. The cause may be a mere bias of the sample that may have not preserved bones of different morphotypes, if they ever existed. As for the coracoids, only future discoveries will help to solve this problem.

In summary, the number of morphotypes found (from 1 to 4) hints at the existence of more than one species within the Peirópolis material. Of all bone categories which have yielded two morphotypes (scapula, sternal plate, ulna, femur and fibula), these are different enough from each other to be promptly recognized. Among the bone categories for which three morphotypes were identified (radius, pubis, ischium), at least two of them are morphologically similar to each other (morphotypes 1 and 2 radii; morphotypes 1 and 2 ischia and morphotypes 1 and 3 pubes); but are quite different from the remaining morphotypes (morphotype 3 radius; morphotype 3 ischium, and morphotype 2 pubis).

This suggests that the Peirópolis material is composed of at least two different species, with a third taxon representing either a third species or a morphological variation of one of the formers, perhaps caused by sexual dimorphism.

This hypothesis supports previous works, which also have concluded for the existence of two or three species within the Peirópolis material (POWELL, 1987a; CAMPOS & KELLNER, 1999).

FAUNAL DIVERSITY AMONG THE THREE MAIN COLLECTING SITES

The results of this item are listed in Table 40.

The analysis has shown rather confusing results in this respect. There is no set of morphotypes that is exclusive of one site alone. The discussion below focus only in bone categories where different morphotypes have been detected.

The sample of "Rodovia" site is meager, but the morphotypes found there appear also in ether one of the two other sites. That is the case for the sternal plate, ulna and radius morphotypes (which are also found in Site 1), and for the fibula morphotype (also found in "Galga").

Site 1 has yielded a mixture of two morphotypes in some bone categories: sternal plates, ulna and radius. This list could be extended in the future, if part of the material

scored as "Peirópolis surroundings" would be confirmed as of Site 1 origin. The diversity of morphotypes found in Site 1 is probably related to the size of the sample, since this site has yielded a greater amount of remains than the other two sites (including some bones of "Peirópolis surroundings" list).

The "Galga" site has yielded only one morphotype in some bone categories: scapula, sternal plate, ischium and femur. The bone categories in which more than one morphotype has been found are the radius, pubis and fibula.

In "Galga" site are found some morphotypes that are not found in any of the other two sites. These are the morphotype 2 pubes, the morphotype 1 ischium and the morphotype 3 radius. These are the only morphotypes, which have been exclusively related to a single site. But the presence, in "Galga", of some morphotypes that are also found in Site 1 (radius, fibula) or "Rodovia" (fibula); suggest that the preservation of these exclusive material may have been occasional.

We concluded, thus, that there is not faunal diversity among the three main collection sites.

PRESENCE OF SYNAPOMORPHIES

There are several synapomorphies described in previous works dealing with Sauropod phylogeny (WILSON & SERENO, 1998; SALGADO *et al.*, 1997a; SANZ *et al*, 1999). The majority of them are related to cranial and vertebral characters. From the synapomorphies related to the appendicular skeleton, the majority of them is placed in basal nodes of the given cladograms, and is useful only in diagnosing the Sauropoda itself, or other lowest taxa, such as the Neosauropoda, and the Eusauropoda.

For instance, in the analysis of WILSON & SERENO (1998), from a total of 104 listed synapomorphies, half of them (52) are related to the appendicular skeleton. From these 52, a total of 37 are place below the Neosauropoda level. Their Somphospondyli (*Euhelopus* + Titanosauria) is diagnosed by 5 synapomorphies, from which only one is related to the appendicular skeleton.

From the 52 synapomorphies listed for the appendicular skeleton, only 19 are related to girdle elements (excluding the ilium) and limb bones (excluding the manus and pes).

From WILSON & SERENO, 1998:

(numbers indicate synapomorphies, number in parenthesis indicate synapomorphies related to appendicular skeleton, immediately followed by number of synapomorphies of girdle and limb bones alone).

Sauropoda 17 (16-8)
Eusauropoda 40 (16-4)
Barapasaurus + *Omeisaurus* + Neosauropoda 7 (3-1)
Omeisaurus + Neosauropoda 10 (2-1)
Neosauropoda 12 (7-1)
Macronaria 3 (1-1)
Camarasaurus + Titanosauriformes 7 (3-1)
Titanosauriformes 5 (3-1)
Somphospondyli (*Euhelopus* + Titanosauria) 5 (1-1)

Total number of synapomorphies: 104
Number of synapomorphies related to appendicular skeleton: 52
Number of synapomorphies related only to girdle and limb bones: 19

From SALGADO, CORIA & CALVO, 1997a
(numbers indicate synapomorphies, number in parenthesis indicate synapomorphies related to appendicular skeleton).

In the phylogenetic analysis made by these authors, from a total of 46 synapomorphies, only 20 are related with the appendicular skeleton. Within the Titanosauridae, from a total of 8 synapomorphies, 4 are related to the appendicular skeleton. Above the Titanosauridae level, however (Taxon II to Taxon VI, and the Saltasaurinae) this number drops to 3 in a total of 12.

Sauropoda 5 (3-1)
Eusauropoda 2 (2-2)
Neosauropoda 2 (0-0)
Camarasauromorpha 5 (2-1)
Titanosauriformes 6 (4-1)

Taxon I 1 (1-1)

Titanosauria 5 (1-1)

Titanosauridae 8 (4-1)

Taxon II to VI 9 (3-3)

Saltasaurinae 3 (0)

Total number of synapomorphies: 46

Number of synapomorphies related to appendicular skeleton: 20

Number of synapomorphies related only to girdle and limb bones: 11

From SANZ *et al.*, 1999

(numbers indicate synapomorphies, number in parenthesis indicate synapomorphies related to appendicular skeleton).

In the work of SANZ *et al.* (1999), from a total of 43 characters, only 14 were related to appendicular skeleton. Only the more important clades are listed below.

Clade I 5 (2-2)

Titanosauroidea 7 (4-3)

Titanosauria 5 (2-2)

Eutitanosauria 4 (1-1)

Total number of synapomorphies: 43

Number of synapomorphies related to appendicular skeleton: 14

Number of synapomorphies related only to girdle and limb bones: 12

All this data hints at the great potential of further studies on sauropod appendicular bones.

DIAGNOSIS OF THE PEIRÓPOLIS MATERIAL

After the morphological analysis undertaken, and taking into consideration the presence of synapomorphies listed in the main systematic works of WILSON & SERENO

(1998); SALGADO, CORIA & CALVO (1997a) and SANZ *et al.* (1999), the Brazilian fossils may be diagnosed as follows (numbers indicate the character numbers given by those authors in their respective works):

SAUROPODA:

From WILSON & SERENO (1998)

3. Humeral deltopectoral crest low
5. Ulna proximal end triradiate, with deep radial fossa
6. Radial distal condyle subrectangular with flat posterior margin for ulna.
8. Ischial shaft equal to, or longer than pubic shaft
9. Ischial shaft with dorsoventrally flattened distal end
10. Femoral shaft with elliptical cross section, long axis of ellipse oriented mediolaterally
11. Femoral fourth trochanter developed as a low crest

From SALGADO, CORIA & CALVO (1997a)

3.Ilium with pubic peduncle much longer than ischiatic articulation
4. Femur nearly straight in lateral view

EUSAUROPODA:

From WILSON & SERENO (1998)

46. Pubic apron canted posteromedially
47. Tibial cnemial crest projecting laterally
48. Tibial posteroventral process reduced
49. Fibular lateral trochanter

From SALGADO, CORIA & CALVO (1997a)

6. Anterior trochanter of femur absent

Barapasaurus + *Omeisaurus* + NEOSAUROPODA

62. Fibula with broad triangular articular scar for tibia (WILSON & SERENO, 1998)

NEOSAUROPODA:

83. Tibia with subcircular proximal end (WILSON & SERENO, 1998)

MACRONARIA:

88. Ischial distal shafts platelike and nearly coplanar (WILSON & SERENO, 1998)

CAMARASAUROMORPHA:

95. Puboischial contact deep dorsoventrally (WILSON & SERENO, 1998); same as:
13. Dorsoventrally extended pubic articulation of ischium (SALGADO *et al.*, 1997a)

TITANOSAURIFORMES:

100. Femur with proximal one-third of shaft deflected medially (WILSON & SERENO, 1998), same as:
19. Presence of a prominent lateral bulge in femur, below greater trochanter (SALGADO *et al.* 1997a).

SOMPHOSPONDYLI (*Euhelopus* + Titanosauria):

104. Scapular glenoid deflected medially (WILSON & SERENO, 1998)

TITANOSAUROIDEA:

From SANZ *et al.*, (1999)
35. Prominent and medially twisted deltopectoral crest of humerus
36. Well developed posterior supracondylar ridges of the humerus
40. Lateroproximal buttress of femur

TAXON I ((*Jubutisaurus insignis* + Titanosauria):

7(-). Distal end of tibia broader transversely than anteroposteriorly (SALGADO *et al.*, 1997a).

TITANOSAURIA:

24*. Pubis considerably longer than ischium (SALGADO *et al.*, 1997a).

From SANZ *et al.* (1999)

30. Antero-ventral ridge in sternal plate

39.2. Short, laminar ischiatic process of ischium

EUTITANOSAURIA:

41. Reduced fourth trochanter in femur (SANZ *et al.*, 1999)

TITANOSAURIDAE:

26*. Semilunar sternal plates (SALGADO *et al.*, 1997a).

TAXON II (Taxon III + Taxon V):

29. Quadrangular coracoids (SALGADO *et al.*, 1997a).

TAXON V (*Aelosaurus* + Taxon VI):

33. Presence of dorsal prominence on inner face of scapula (SALGADO *et al.*, 1997a).

Among the Brazilian material, this character is detected only in morphotype 2 scapulae.

The diagnosis of the Brazilian material cannot go further, because, above this taxon, there is only one character related to the pelvic girdle (n° 36, see below), while all

others (including all synapomorphies of the Saltasaurinae) are related to vertebral elements.

TAXON VI (*Alamosaurus sanjuanensis* + SALTASAURINAE):

SALGADO *et al.* (1997a: 24) have defined a synapomorphy of this clade (n° 36 – relatively short posterior process of ischium).

This character was already discussed in the morphological analysis of the ischium (Table 32). The analysis has shown that the length of the posterior process of ischium varies among the ischia from Peirópolis. Although none of them display this character, MCT 1689 approaches the derived condition (C/D ratio = 0,47), while MCT 1655 and 1661 are primitive (C/D ratio ~ 0,41).

The presence of character n° 33 in the Peirópolis scapulae (only in morphotype 2) and of character n° 36 suggest that some of the Brazilian bones belonged to a Titanosauridae with Taxon V affinities, more closely related to the genus *Aelosaurus* than to the Taxon VI members. The presence of other morphological similarities between *Aelosaurus* and the Brazilian bones (presence of a longitudinal ridge on the pubic apron, presence of an elevation on the deltopectoral crest of humerus) reinforces this hypothesis. The absence of Saltasaurinae affinities was already observed in the vertebral elements (POWELL, 1987a)

In summary, from a total of 42 possible synapomorphies related exclusively to girdle and limb bones, 33 are present in the Peirópolis material. These synapomorphies allow us to diagnose the Peirópolis bones as Sauropoda, Titanosauria, of the family Titanosauridae (including here also the evidence from pelvic and vertebral characters).

This obviously excludes the existence, among the girdle and limb bones, of remains of other dinosaur clades, such as the Theropoda and the Ornithischia, as well as of non-titanosaurian sauropods.

The affinities of the Peirópolis material with other Titanosauridae members, as well as its position in relation to the Saltasaurinae (from which it is excluded), will only be possible after the detailed study of the vertebral remains and the definition of which bone belong to which species.

MORPHOLOGICAL FEATURES OF THE BRAZILIAN MATERIAL

The morphological analysis undertaken so far has shown that the girdle and limb bones from Peirópolis display both similar and unique morphological features in relation to other titanosaurian species from different parts of the world.

Among some important features shared by both Brazilian and foreign species are:

Presence of a medial prominence in morphotype 2 scapulae, that may be homologous to a prominence bore by the Argentinean genera *Aelosaurus*, *Saltasaurus* and *Titanosaurus* (=*Neuquensaurus*); by the North American species *Alamosaurus sanjuanensis*, and by *Lirainosaurus astibiae* from Europe.

With this last species, the Brazilian sternal plates share the presence of a latero-anterior process, a feature that was previously regarded as an autapomorphy of the Spanish species. The Brazilian sternal plates also bear a prominent antero-ventral ridge, as *Lirainosaurus*, *Alamosaurus* and some Argentinean genera (*Saltasaurus*, *Titanosaurus* = *Neuquensaurus*).

The coracoids and scapulae of Brazil are similar, in overall shape to the coracoid of *Alamosaurus sanjuanensis*. As in the North American species, they are not fused to each other, differentiating them from the Argentinean Saltasaurinae and the Asiatic *Opisthocoelicaudia skarzynskii*.

The humeri from Peirópolis are similar in overall shape and proportions to some Argentinean genera (*Aelosaurus* and *Argyrosaurus*), and to *Alamosaurus*. But they are differentiated from the Argentinean Saltasaurinae and the Asiatic, *Opisthocoelicaudia* and *Titanosaurus colberti* by the relative proportions of the humeral head (length and breadth) in relation to total length of shaft.

The ulnae from Peirópolis are similar to other titanosaurid ulnae in general, bearing a prominent, developed olecranon. This olecranon is non-divided, approaching the morphology of other Argentinean taxa (*Titanosaurus* =*Neuquensaurus australis*, and *Aelosaurus*).

The radii of Peirópolis are very stout, which is a normal trait of the Titanosauridae (McINTOSH, 1990). Those of morphotypes 1, 2 and are similar in overall shape to the majority of Argentinean taxa (*Aelosaurus*, and the Saltasaurinae) and to *Alamosaurus sanjuanensis* (USA). The morphotype 3 radius (especially MCT 1707-R) is similar to the radius of *Laplatasaurus araukanicus*. The radius of *Opisthocoelicaudia skarzynskii* (Asia)

is more robust than the Brazilian ones. Radii of European and African species are not known or described.

The pubes of morphotypes 1 and 3 of Peirópolis share some traits with Argentinean and Asiatic forms. These pubes (particularly morphotype 1), are very similar to *Aelosaurus* pubis in having a well-developed longitudinal ridge running along the lateral surface of the pubic apron. The pubis of morphotype 3 shares with *Opisthocoelicaudia skarzynskii* the vertical anterior surface of the iliac pedicle.

The ischia of morphotypes 1 and 2 of Peirópolis are similar to the ischia of *Aelosaurus* (Argentina) and *Opisthocoelicaudia skarzynskii* (Asia) by having long and non-laminar distal shafts. In this respect, they are all distinct from the short and laminar distal shafts present in *Andesaurus delgadoi* and the Saltasaurinae (Argentina), *Alamosaurus sanjuanensis* (USA), *Malawisaurus dixeyi* (Africa) and *Titanosaurus colberti* (Asia). The ischia of these taxa are, in turn, more similar to Peirópolis ischium MCT 1689-R (morphotype 3).

The femora from Peirópolis display the normal titanosauriform morphology, that is, its upper third is medially deflected (SALGADO *et al.*, 1997a – character n° 19; WILSON & SERENO, 1998 – character n° 100), and the fourth trochanter is reduced (SANZ *et al.* 1999 – character n° 41).

The tibiae from Peirópolis are similar in general morphology to the titanosaurian pattern by having its distal end broader transversely than anteroposteriorly (SALGADO *et al.*, 1997a – character n° 7).

The fibulae from Peirópolis are also similar in general morphology to the titanosaurian pattern. An exception could be the medial oblique ridge bore by morphotype 2 fibulae, but this trait needs to be more investigated among other titanosaurian species.

Among the unique features displayed by the Brazilian specimens are:

The largest scapulae (MCT 1708-R and MCT 1709-R) bear upper expansions on the superior distal border of the blade which are not present in any other known titanosaurid. The coracoid MCT 1691-R bears a distinct protuberance on its superior anterior corner, which may be an unique trait of this bone alone

The sternal plates of morphotype 1 display a rather triangular profile in anterior view that seems to differ from other titanosaurian species described. This character must be further investigated, since most of sternal plates described elsewhere (for instance:

Alamosaurus, *Malawisaurus*, *Saltasaurus*, *Lirainosaurus*) have not been figured in this view. The latero-anterior process, although not unique to the Peirópolis material (for this trait is also present in *Lirainosaurus astibiae*), should be mentioned here, since it is absent from all other known Argentinean titanosaurids.

The presence of a longitudinal elevation on the deltopectoral crest of the humerus is a trait that is only present in the Brazilian bones and in *Aelosaurus*.

The distal excavation bore by morphotype 1 ulnae from Peirópolis is not reported in any other known titanosaurid. An exception could be *Alamosaurus sanjuanensis* (USA), whose ulna is said to be reniform in distal view (GILMORE, 1946: 37).

Peirópolis pubes of morphotype 2 are unique among titanosaurid pubes in having a slope on the anterior margin, separating the pubic apron from the iliac pedicle. The shape of this pedicle varies in the Brazilian material, but comparisons with other species are hindered by the lack of figures depicting the bone in proximal view.

Ischia of morphotype 1 bear a reentrance under the ischial blade that is absent from all other known titanosaurids. Among other sauropods, a similar trait is found in the ischium of *Camarasaurus* (WILSON & SERENO, 1998: 28, fig.29A). This suggests that this trait may be a primitive condition retained in the Brazilian specimen.

The fibulae from Peirópolis are similar in overall shape to the fibulae of other known titanosaurids. Nevertheless, the medial oblique ridge present in Brazilian morphotype 2 fibulae may be an unique trait. More data on fibular anatomy (especially from the Argentinean species) is needed before we can say anything more precise about this bone.

MORPHOLOGICAL VARIATION SURVEY

The morphological analysis undertaken just on the girdle and limb bones of Peirópolis resulted in the identification of many morphological characters for each of the eleven bone categories included in this study. Many of this characters have shown variation, not only in the sample itself, but also among other known titanosaurid species. Some examples are mentioned just below.

In the scapula, a medial prominence is present in some taxa, and even when present, its morphology seems to vary. The distal blade shape may vary, bearing upper expansions or not. In the plate, the acromion varies in length, and an indentation for

reception of the coracoid may be either well marked or not. The coracoid itself may be either fused to the scapula or not (although this may be only caused by ontogenetic factors), and the presence of other morphological features (such as an medial oblique elevation, overall proportions) must be further studied in other sauropods.

The sternal plates have shown variation in possessing either a latero-anterior process or an antero-ventral keel. The last may give the plate either a triangular or a "T" shaped profile in anterior view. The plates also vary in breadth among different titanosaurid species.

The humerus has shown variation in the proportion of the humeral head (length and breadth) in relation to total length of shaft. In the Saltasaurinae and *Opisthocoelicaudia skarzynskii*, the humeral head extends itself down below the shaft, reaching almost its middle, and its breadth is proportionally great in relation to total length of the shaft. In the Peirópolis material, as well as in *Alamosaurus* and *Argyrosaurus*, the humeral head makes about 40% of total length of the shaft, and is proportionally narrower. *In Titanosaurus colberti*, the humeral head contributes to at about a third of its total length, and is the narrowest.

The ulna is rather conservative in shape, but overall robustness, the shape of its olecranon (undivided or divided by a notch), the presence or absence of a distal excavation on its radial face and relative development of the lateral and medial processes are characters that have shown some variation among different titanosaurids.

The radius has shown to be source for several characters: development of the anteromedial projection (pointed or well-developed), morphology of distal articular area for ulna (ovoid or not, with or without a microridge) and presence of longitudinal ridges other than the *interosseus* ridge (either single or doubled).

The pubis has shown considerably variation in the morphology of its iliac pedicle, either on its anterior margin (with a slope, continuous with anterior margin of pubic apron or vertically oriented above the *ambiens* scar) or on its iliac articular margin (medio-laterally flattened or expanded, triangular shaped). These characters must be surveyed in other titanosaurid species, for most works do not figure the pubis in proximal view. The pubic apron may bear either a longitudinal ridge (as in *Aelosaurus*) or not.

Among ischia, the presence or absence of a reentrance under the ischial blade, and shape of distal shaft (long or narrow, laminar or non-laminar) are important characters to be ever taken into consideration. The presence or absence (and relative development) of

the process of muscle *flexor tibialis* is a character that still must be surveyed among titanosaurids.

The femur shows poor variation, unless for its overall shape (robust or slender). This limb element must be more studied yet.

The tibiae show variation in overall robustness, shape of distal end, shape of cnemial crest and to which degree the head is twisted in relation to the distal end (SANZ *et al*., 1999 – character n° 42). Presence of a digitiform depression on inner surface of the cnemial crest is a character still to be observed among other titanosaurid tibiae.

In the fibula, the presence or absence of an anterior trochanter; shape of the lateral trochanter (divided or not) and presence or absence of a medial oblique ridge are important features to be considered in future studies.

The present work shows that comparative morphological studies on sauropod girdle and limb bones have good potential to yield a great amount of new data. These data may be very profitable in tracing new phylogenetic hypotheses regarding the Titanosauridae, as well as the Sauropoda in general, improving our present knowledge about those extinct animals.

CONCLUSION

After the close of the present study, we have reached the following conclusions:

MORPHOLOGICAL VARIATION WITHIN THE MATERIAL

The girdle and limb bones from Peirópolis do shown morphological variation in most of the bone categories studied, which were separated into 2 (scapula, sternal plate, ulna, femur, fibula), 3 (pubis, ischium) or 4 (radius) distinct morphotypes. The coracoids were not separated into morphotypes, but show morphological variation anyway. The humerus and tibia display one single morphology, and this was interpreted either as non-existence of different morphotypes for these categories, or as a limitation of the sample.

Among the categories, which have been separated in 3 morphotypes, two of them are morphologically similar, and the third is quite different from them.

The morphological evidence hints at the existence, in the sample, of either three distinct species or two species and a dimorphic form (perhaps related to sex) belonging to one of the two.

FAUNAL DIVERSITY AMONG THE THREE MAIN COLLECTING SITES

The study has shown that there is no set of morphotypes exclusive for one single site. In "Galga" and Site 1 there is a mixture of at least two morphotypes, for certain bones. The "Rodovia" site has no mixture of morphotypes, but the remains there are too meager. Besides, its morphotypes also appear in ether one of the two other sites.

Site 1 has yielded the greatest amount of bones (including articulated vertebral series and two pelves), and is the only site represented by a field map. This map clearly indicates the presence of more than one individual in that sample. The smallest bones came from this site, attesting the presence of very young individuals there.

Also the two other sites are composed by a mixture of individuals, which is attested by the presence of bones from the same side of the body (right or left) or of different sizes (indicating individuals of different ages).

So, all three sites represented part of the living population, and are not related to any particular fauna of their own.

PRESENCE OF SYNAPOMORPHIES

From a total of 42 possible synapomorphies related exclusively to girdle and limb bones, 33 are present in the Peirópolis material. The presence of these synapomorphies diagnose the Peirópolis material as Sauropoda, Titanosauria, Titanosauridae (non-Saltasaurinae).

MORPHOLOGICAL FEATURES OF THE BRAZILIAN MATERIAL

The girdle and limb bones from Peirópolis display both similar and unique morphological features in relation to other titanosaurian species from different parts of the world, especially with the Argentinean genus *Aelosaurus*.

Unique features of the Brazilian material include: upper expansion on superior border of scapular blade; anterior protuberance of coracoid MCT 1691-R; anterior triangular profile of morphotype 1 sternal plates; presence of latero-anterior process in all sternal plates (only shared with *Lirainosaurus astibiae*); elevation on deltopectoral crest of humerus (only shared with *Aelosaurus*); distal excavation on morphotype 1 ulnae; anterior slope below *ambiens* scar in morphotype 2 pubes; reentrance under ischial blade of morphotype 1 ischia; medial oblique ridge of morphotype 2 fibulae.

MORPHOLOGICAL VARIATION SURVEY

The present work has suggested that girdle and limb bones display morphological variation that may be the source for the discovery of new characters, which may be potentially useful in building new phylogenetic hypotheses regarding the Titanosauridae.

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ABSTRACT

MORPHOLOGY OF THE APPENDICULAR SKELETON AND OF THE PECTORAL AND PELVIC GIRDLES OF THE TITANOSAURIDAE (DINOSAURIA, SAUROPODA) FROM THE LATE CRETACEOUS OF MINAS GERAIS, BRAZIL

Seventy-two appendicular and girdle bones referred to the family Titanosauridae (Dinosauria: Sauropoda) are described and figured. They have been found in Continental Upper Cretaceous strata of Brazil (Bauru Basin), near the city of Peirópolis, state of Minas Gerais. All of them were collected, together with vertebrae and three pelves, from 1947 to 1974 by L.I. Price, who passed away before he could study them. The material comes from three main sites: "Site 1 or Caieira", "Rodovia", and "Serra da Galga". The bones which are not referable to any of these sites, or are isolated findings, have been scored as Peirópolis surroundings". The study detected morphological variation in most of the bone categories, which were separated into 1 (coracoid, humerus, tibia), 2 (scapula, sternal plate, ulna, femur, fibula), 3 (pubis, ischium) or 4 (radius) distinct morphotypes. The morphotypes are widespread among the three main collecting sites. From a total of 42 possible synapomorphies described in the literature, which are related exclusively to girdle and limb bones, 33 are present in the Peirópolis material. The presence of these synapomorphies diagnose this material as Sauropoda, Titanosauria, Titanosauridae (non-Saltasaurinae). The bones from Peirópolis were preliminary compared with other titanosaurid species of the world, especially from Argentina. They show both similar and unique morphological features in respect to other titanosaurid species.

Key words: Sauropoda, Titanosauridae, Bauru Group, Cretaceous.

RESUMO

MORFOLOGIA DO ESQUELETO APENDICULAR E DAS CINTURAS PEITORAL E PÉLVICA DOS TITANOSAURIDAE (DINOSAURIA, SAUROPODA) DO NEOCRETÁCEO DE MINAS GERAIS, BRASIL

Setenta e dois ossos fossilizados referidos ao clado Titanosauridae (Dinosauria: Sauropoda) são descritos e ilustrados. Os exemplares são procedentes dos depósitos do Cretáceo Superior continental do Brasil (Bacia Bauru), próximos à localidade de Peirópolis, no estado de Minas Gerais. Todos foram coletados, juntamente com vértebras e três cinturas pélvicas, entre os anos de 1947 e 1974, por L.I. Price, que faleceu antes de poder descrevê-los. O material foi recolhido em três localidades principais: "Localidade 1 ou Caieira", "Rodovia" e "Serra da Galga". Os ossos que não puderam ser associados a nenhuma dessas três origens, ou que representam achados isolados, foram registrados como "Cercanias de Peirópolis". O estudo detectou variação morfológica na maioria das categorias de ossos, que foram separadas em 1 (coracóide, úmero, tíbia), 2 (escápula, placa esternal, ulna, fêmur, fíbula), 3 (púbis, ísquio) ou 4 (rádio) morfótipos distintos. Os morfótipos estão distribuídos pelos três principais locais de coleta. De um total de 42 sinapomorfias descritas na literatura, relacionadas exclusivamente a ossos apendiculares e das cinturas peitoral e pélvica, 33 estão presentes no material de Peirópolis. A presença dessas sinapomorfias permitem diagnosticar o material como pertencente a Sauropoda, Titanosauria, Titanosauridae (não-Saltasaurinae). Os ossos de Peirópolis foram preliminarmente comparados com outras espécies de titanossaurídeos do mundo, especialmente da Argentina. Eles apresentam características morfológicas tanto similares quanto próprias em relação a outras espécies.

Palavras-chave: Sauropoda, Titanosauridae, Grupo Bauru, Cretáceo.

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TABLES

Table n° 1: Fossil bones from "Serra da Galga" site.
(* indicates exclusion of the present work)
DAC = information given by Diógenes A .Campos

N° MCT	Category	Provenance	Collecting date	Notes
1585-R	Ischium	Serra da Galga	1971	-
1586-R	Ischium	"	"	-
1587-R	Tibia (frag.)	"	1972	Prox./distal
1588-R	Fibula	"	"	-
1589-R	Sternal plate	"	"	-
1591-R	Pubis	"	"	-
1592-R	Pubis	"	1971	Titanosauridae A?
1595-R	Radius	"	1973	-
1597-R	Humerus	"	Seventies	-
1598-R	Radius	"	Seventies	-
1599-R	Scapula (frag.)	"	1972	Only proximal part
1600-R	Coracoid	"	"	-
1601-R	Femur	"	"	-
1602-R	Coracoid	"	"	-
1606-R*	Metapodial	"	1967	North of Uberaba
1695-R	Tibia	Serra da Galga ?	"	DAC
1696-R	Fibula	Serra da Galga	1967	Largest
1711-R	Pubis	"	1971	Largest

Table n° 2: Fossil bones from "Rodovia" site.
(* indicates exclusion of the present work)

N° MCT	Category	Provenance	Collecting date	Notes
1607-R	Fibula	Rodovia	1967	Only proximal part
1608-R	Fibula	"	"	
1609-R	Ulna	Rodovia?	?	
1610-R	Radius	Rodovia	1967 or 1969	
1611-R	Pubis (frag.)	"	1969	
1614-R *	Metacarpal	"	"	
1627-R *	Metacarpal	"	"	
1698-R	Sternal plate	"	?	

Table n° 3: Fossil bones from Site 1 or "Caieira".
(* indicates identification by a photo taken by L.I.Price)

N° MCT	Category	Provenance	Collecting date	Notes
1648-R	Radius	Peirópolis Site 1?	1958	
1649-R	Radius	Peirópolis Site 1?	1959	
1650-R	Radius	Site 1	?	
1651-R	Ulna	"	?	
1652-R	Scapula	"	?	
1653-R	Coracoid	"	?	
1654-R	Ischium	"	1959	
1655-R	Ischium	"	1959	
1657-R	Fibula	"	1959	
1659-R	Ulna	"	?	
1660-R	Fibula	"	1959	
1661-R	Ischium	"	1959	
1674-R*	Humerus	"	?	Photo
1688-R	Humerus	"	?	One of the largest
1713-R	Sternal plate	"	1958	Smallest, complete

Table n° 4: Fossil bones recorded as from "Peirópolis surroundings". (DAC = information given by Diógenes A. Campos)

N° MCT	Category	Provenance	Collecting date	Notes
1635-R	Ulna	Peirópolis (surroundings)	1959?	
1636-R	Radius	"	?	
1637-R	Radius	"	?	
1638-R	Radius	"	?	
1639-R	Scapula	"	?	
1640-R	Pubis	"	?	
1641-R	Pubis	"	?	
1642-R	Scapula	"	?	
1673-R	Radius	Peirópolis (1km N)	?	Prox./dist. frag.
1675-R	Pubis	Peirópolis (surroundings)	?	
1676-R	Ulna	"	?	
1677-R	Pubis	"	?	
1678-R	Ulna	"	?	
1679-R	Ischium	"	?	
1680-R	Scapula	"	?	
1681-R	Tibia	"	?	
1682-R	Humerus	"	?	DGM 811 LE
1683-R	Tibia	"	?	
1684-R	Humerus	"	?	
1689-R	Ischium	"	?	Possibly associated with a pelvis (DAC)
1690-R	Sternal plate	"	?	Possible Site 1
1691-R	Scapula and Coracoid	"	?	DAC
1692-R	Femur	"	?	
1693-R	Femur	Peirópolis ?	?	
1694-R	Femur	Peirópolis	?	
1703-R	Scapula and Coracoid	"	?	DGM 810 LE
1708-R	Scapula	"	?	Large
1709-R	Scapula	"	?	Largest
1710-R	Coracoid	"	?	Largest
1712-R	Femur	Peirópolis?	?	Largest

Table n° 5: Fossil bones from "Bauru" Group strata. (DAC = information given by Diógenes A . Campos)

N° MCT	Category	Provenance	Collecting date	Notes
1707-R	Radius	São Paulo ?	?	Bauru group (DAC)

Table n° 6: Fossil bones from Uberaba.

N° MCT	Category	Provenance	Collecting date	Notes
547-R	Humerus	Well in the city of Uberaba (MG), Hospital São Paulo Av. Pres. Vargas, 24	1968? Coletor: Dr. Freud Gomes (Donation to DNPM)	Various bones, probably belonging to a single individual

Table n° 7: Number of fossil bones for each bone category. The bones which have been brought to Museu Nacional/RJ for sudy are indicated in the column MNRJ. The remaining bones, which were too heavy or too fragile for transportation have been studied in the DNPM/RJ facilities, and are indicated in the second column.
(* = including humerus MCT 547-R)

Category	MNRJ	DNPM	Totals
Scapulae	6	3	9
Coracoids	4	2	6
Sternal plates	1	3	4
Humeri (*)	5	1	6
Radii	9	2	11
Ulnae	6	-	6
Pubes	7	1	8
Ischia	6	1	7
Femora	1	4	5
Tibiae	3	1	4
Fibulae	5	1	6
Total	53	19	72

Table n° 8 : Bone categories present in "Serra da Galga" site.

Category	MCT n°
Scapula (1)	1599
Coracoid (2)	1600 and 1602
Sternal plate (1)	1589
Humerus (1)	1597
Ulna (0)	-
Radius (2)	1595 and 1598
Pubis (3)	1591 and 1592 (pair)
	1711
Ischium (2)	1585 and 1586 (pair)
Femur (1)	1601
Tibia (2)	1587 (small), 1695 (large)
Fibula (2)	1588, 1696 (largest)
Metapodial (1)	1606

Table n° 9: Bone categories present in "Rodovia" site.

Category	MCT n°
Scapula (0)	-
Coracoid (0)	-
Sternal plate (1)	1698
Humerus (0)	-
Ulna (1)	1609
Radius (1)	1610
Pubis (1)	1611 (fragment)
Ischium (0)	-
Femur (0)	-
Tibia (0)	-
Fibula (2)	1607 and 1608 (both right)
Metacarpals (2)	1614 and 1627

Table n°10: Bone categories present in Site 1 or "Caieira".
(* provenance indicated by photo taken by Price)

Category	MCT n°
Scapula (1)	1652 (pair with 1639)
Coracoid (1)	1653
Sternal plate (1)	1713
Humerus (2)	1674 * and 1688
Ulna (2)	1651 and 1659 (pair with 1676?)
Radius (3)	1648 and 1649 (by collecting date),
	1650
Pubis (0)	-
Ischium (3)	1654
	1655 and 1661 (pair)
Femur (0)	-
Tibia (0)	-
Fibula (2)	1657 and 1660 (pair?)
Metapodials	Several, still unnumbered

Table n° 11: Bone categories recorded a from "Peirópolis surroundings".
(S1? = probably from Site 1 or "Caieira")

Category	MCT n°
Scapula (7)	1639 (S1?)
	1642, 1680, 1691 and 1703
	1708 and 1709 (largest)
Coracoid (3)	1691 and 1703 (both articulated with scapulae)
	1710
Sternal plate (1)	1690 (S1?)
Humerus (2)	1682 and 1684
Ulna (3)	1635 (S1?)
	1676 (S1?)
	1678 (pair with 1635?)
Radius (4)	1636, 1637 and 1638
	1673 (1KmN)
Pubis (4)	1640
	1641 and 1675 (pair)
	1677
Ischium (2)	1679 (pair with 1654?)
	1689
Femur (4)	1692, 1694
	1693? and 1712?
Tibia (2)	1681
	1683
Fibula (0)	-

Table n° 12: Peirópolis bones probably from Site 1 or "Caieira".

Category	MCT n°
Scapula (1)	1639
Sternal plate (1)	1690
Ulna (3)	1635, 1676 and 1678 (pair with 1635?)
Radius (2)	1637 and 1638
Pubis (3)	1640,
	1641 and 1675 (pair)
Ischium (1)	1679 (pair with 1654?)

Table n° 13: Available taxa for morphological comparisons - pectoral girdle and anterior limb.

Taxon	Scapula	Coracoid	Sternal pl.	Humerus	Radius	Ulna	Carpals	Metacarpals
Aelosaurus rionegrinus	Both inc.	-	-	Both	Both	Both	-	I-V
Aelosaurus sp. (2 indiv.)	-	-	incomplete	Left	Right	Right	-	1
Alamosaurus sanjuanensis	Left	Left	Both	Right	Right	Right	-	I-V
Ampelosaurus atacis	2	3	2	6	3	1	-	-
Andesaurus delgadoi	-	-	-	Distal part	-	-	-	-
Antarctosaurus brasiliensis	-	-	-	Right frag.	-	-	-	-
Antarctosaurus giganteus	-	-	-	-	-	-	-	-
Antarctosaurus wichmannianus	Left	-	-	Right inc.	2 incompl.	Left inc.	-	I-V + phalanges
Argentinosaurus huinculensis	-	-	-	-	-	-	-	-
Argyrosaurus sp.	Left	-	-	Left	Right/left	Right/left	-	-
Argyrosaurus superbus holotype	Left	-	-	Left	Left	Left	-	I-V
Chubutisaurus insignis	-	-	-	Left	Left	Left	-	4
Gondwanatitan faustoi	Left prox.	-	-	Both	-	-	-	-
Laplatasaurus araukanicus	Right/left	-	Left	Left	Right/left	Right	-	I-V + phalanges
Laplatasaurus sp. = Antarctosaurus sp.	-	-	-	Right inc.	Right	Right	-	
Lirainasaurus astibiae	Left	Right	Frag.	Both	-	-	-	-
Malawisaurus dixeyi	?	-	Both	-	-	-	-	-
Opisthocoelicaudia skarzynskii	Both	Both	Both	Both	Both	Both	-	I-IV
Rocasaurus muniozi	-	-	-	-	-	-	-	-
Saltasaurus loricatus (5 individuals))	4	3	4	10	4	5	-	5
Titanosaurinae from Guararapes	-	-	-	Left prox.	-	-	-	-
Titanosaurus australis	Right/left	Right/left	Right/left	Right/left	Right/left	Right/left	-	II, IV + phalanges
Titanosaurus colberti	Left	Left	-	Left	-	Left	-	-
Titanosaurus robustus	-	-	Left	Right	Left	Right/left	-	-

Table n° 14. Available taxa for morphological comparisons - pelvic girdle and posterior limb.

Taxon	Sacrum	Pubis	Ischium	Femur	Tibia	Fibula	Tarsals	Metatarsals
Aelosaurus rionegrinus	-	-	Both	-	Right	Right	astragalus	-
Aelosaurus sp.	-	Left	Right	Left inc.	Left	Left	Left astrag.	4 left
Alamosaurus sanjuanensis	Left in field	-	Both	-	-	-	-	-
Ampelosaurus atacis	Ilium	1	1	8	4	2	-	
Andesaurus delgadoi	-	Left	Right/left	incomplete	-	-	-	-
Antarctosaurus brasiliensis	-	-	-	Left frag.	-	-	-	-
Antarctosaurus giganteus	-	Frag.	-	Both	Distal end	-	-	-
Antarctosaurus wichmannianus	Ilia frag.	Pubis frag.	Both inc.	Left	Left	Left	Left astragalus, calcaneum	I-IV + phalanges
Argentinosaurus huinculensis	Incomplete	-	-	-	Right inc.	-	-	-
Argyrosaurus sp.	-	-	-	Right	Incomplete	-	-	-
Argyrosaurus superbus holotype	-	-	-	-	-	-	-	-
Chubutisaurus insignis	-	-	-	Left	Left	-	-	-
Gondwanatitan faustoi	Incomplete	Both inc.	Both	Both	-	-	-	-
Laplatasaurus araukanicus	Both ilia	-	-	Right	Right/left	Right/left	-	-
Laplatasaurus sp. = Antarctosaurus sp.	Ilium frag.	Right frag.	Left, frag.	Left	Right	Right	-	-
Lirainasaurus astibiae	Ilium frag.	Frag.	-	Right + 2	Right	Right	-	-
Malawisaurus dixeyi	-	Right?	Left	-	-	-	-	-
Opisthocoelicaudia skarzynskii	Almost complete	Both	Both	Both	Both	Both	Both astragalus	I-V
Rocasaurus muniozi	Left ilium	Left	Both	Left	-	-	-	-
Saltasaurus loricatus (5 individuals)	Holotype	4	2	5	5	4	-	7
Titanosaurinae from Guararapes	-	-	-	Left distal	-	-	-	-
Titanosaurus australis	Ilium	Right	Left	Right/left	Right/left	Right	Right astragalus, calcaneum	I,II,IV,V + phalanges
Titanosaurus colberti	Complete	Both	Right	-	-	-	-	-
Titanosaurus robustus	Left ilium			Right/left	Right/left	Right/left	-	I-V + phalanges

Table n° 15: General data on the scapulae from Peirópolis.

Nº MCT-R	Site	Year	Right/Left	Notes	Morphotype
1599	Galga	1972	Left	Large without distal portion	2
1639	Peiróp. Site1?	?	Right	Smallest, pair with 1652	2
1642	Peiróp.	?	Left	Large, proximal part only	1
1652	Site 1	?	Left	Smallest, pair with 1639	2
1680	Peiróp.	?	Right	mid-size	2
1691	Peiróp.	?	Left	With coracoid	2
1703	Peiróp.	?	Left	Large, with coracoid, DGM 810LE	1
1708	Peiróp.	?	Right	Large	2
1709	Peiróp.	?	Left	Largest	2

Table n° 16: measurements of the scapulae from Peirópolis (in mm):
Dimensions are indicated in Fig. 11
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1599*	MCT 1639	MCT 1642*	MCT 1652*	MCT 1680	MCT 1691*	MCT 1703	MCT 1708*	MCT 1709*
1) Total length	> 565	523	>610	524	590	565	788	>840	~920
2) Length of acromion	~ 260	165	?	175	182	>170	180	~120	>190
3) Length of upper margin	?	> 510	?	> 530	625	>580	654	>700	>720
4) Length of lower margin	?	485	>570	480	553	525	~700	>710	845
5) Total height	395	280	~330	~265	285	345	~410	520	>480
6) Height of acromion	280 (80)	205 (55)	>280 (60)	202 (55)	222 (62)	>275	310 (78)	~360	>370
7) Length of blade	?	327	?	334	392	~325	510	>500	625
8) Distal width of blade	?	~125	?	>125	163	~180	204	~250	~260
9) Length of medial ridge	75	50	Not present	50	55	40	Not present	60	66
10) Minimum width of the blade	134	79	132	85	99	127	138	165	175
11) Position of minimum width of the blade	?	196	?	~192	274	~225	315	>320	450
12) Length of articular border with coracoid	205	150	?	134	175	140	255	340	?
13) Width of glenoid	>120	98	?	>85	114	110	143	215	>160
14) Height of glenoid	195	142	?	140	148	170	~175	265	~180
15)Width of expansion of the blade	?	Not present	?	Not present	Not present	Not present	Not present	215	210

Table n° 17: Evaluation of character n° 72 of Wilson & Sereno (1998).
Numbers in parenthesis correspond to measurements as indicated in Fig. 11.

Scapula MCT n°	Total Length (1)	Length of acromion (2)	Minimum width of blade (10)	150% of (10)	Percentage of (2) in relation to (10)	State of Character n° 72
1639	523	165	79	118,5	208 %	Derived
1680	590	182	99	148,5	184 %	Derived
1691	565	170	127	190,5	134 %	Primitive
1703	788	180	138	207,0	130 %	Primitive
1708	>840	120	165	247,5	73 %	Primitive
1709	~920	190	175	262,5	108 %	Primitive

Table n° 18: General data on the coracoids from Peirópolis.

N° MCT-R	Site	Year	Right/Left	Notes	Morphotype
1600	Galga	1972	Left	Large	1
1602	Galga	1972	Left	Large	1
1653	Site 1?	?	Left	Smallest	1
1691	Peiróp.	?	Left	Mid-size, with scapula	1
1703	Peiróp.	?	Left	Mid-size, with scapula	1
1710	Peiróp.	?	Right	Largest	1

Table n° 19: measurements of the coracoids from Peirópolis (in mm):
Dimensions are indicated in Fig. 12
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1600*	MCT 1602*	MCT 1653	MCT 1691	MCT 1703	MCT 1710*
Length of articular area with scapula	>200	~385	164	210	265	~390
2) Height of anterior border	347	341	155	210	286	295
3) Length of superior border	>190	~255	176	210	277	?
4) Oblique length (internal)	>390	453	227	310	365	~495
5) Length of glenoid	~170	155	87	105	124	125
6) Width of glenoid	186	185	>80	105	143	?
7) Length of coracoidal foramen (external)	45	50	24	30	37	60
8) Width of coracoidal foramen (external)	40	35	20	18	28	40

Table n° 20: General data on the sternal plates from Peirópolis.

N° MCT-R	Site	Year	Right/Left	Notes	Morphotype
1589	Galga	1972	Right	Almost complete	1
1690	Peiróp. Site 1?	?	Left	Complete	2
1698	Rodovia?	?	Left	Too damaged	2
1713	Site 1	1958	Right	Smallest, complete	1

Table n° 21: measurements of the sternal plates from Peirópolis (in mm):
Dimensions are indicated in Fig. 13
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1589*	MCT 1690	MCT 1698*	MCT 1713
1) Length of internal curve	>950	775	1140	700
2) Length of external curve	455	355	600	360
3) Total length	543	~450	660	400
4) Width in the middle	?	~222	?	165
5) Height of ventral keel	~64	~55	?	48
6) Length of keel	115	80	?	60
7) Thickness (distal)	45	29	?	28
8) Thickness of plate	~10	10 to 15	?	05 to 15

Table n°22: General data on the humeri from Peirópolis.

N° MCT-R	Site	Year	Right/Left	Notes	Morphotype
547	Uberaba	1968?	Right	just head	1
1597	Galga	Seventies	Right		1
1674	Peiróp. Site 1	?	Left	Photo taken by Price	1
1682	Peiróp.	?	Left	DGM811LE	1
1684	Peiróp.	?	Right	Large	1
1688	Peiróp. Site 1.	?	Right	Large	1

Table n° 23: measurements of the humeri from Peirópolis (in mm):
Dimensions are indicated in Fig. 14
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 547*	MCT 1597*	MCT 1674	MCT 1682	MCT 1684	MCT 1688
1) Total length	?	616	546	764	610	770
2) Width of head	261	~250	211	302	251	305
3) Height of head	310	325	214	365	260	365
4) Width at middle	~105	90	75	110	95	115
5)Proximal breadth	133	~75	80	120	91	116
6) Width distal end	?	~165	152	222	187	225
7) Distal fore and aft	?	>60	78	122	93	122
8) Medial width	?	>90	110	155	~120	~135
9) Lateral width	?	>50	65	115	91	~98
10) Width fore and aft	83	65	80	75	64	75
11) Height of deltopectoral crest	104	>70	58	120	98	105
12) Length/breadth of prominence	45/9	broken	>25	broken	49/11	>44/9

Table n°24: General data on the ulnae from Peirópolis.

Nº MCT-R	Site	Year	Right/Left	Notes	Morphotype
1609	Rodovia?	?	Right	Mid-size	2
1635	Site 1?	1959?	Left	Largest	2
1651	Site 1	?	Right	Smallest	1
1659	Site 1	?	Right	Mid-size	1
1676	Peiróp.	?	Left	Mid-size	1
1678	Peiróp.	?	Right	Largest	2

Table nº 25: measurements of the ulnae from Peirópolis (in mm):
Dimensions are indicated in Fig. 15
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1609	MCT 1635*	MCT 1651	MCT 1659	MCT 1676*	MCT 1678
1) Greatest length	455	>510	372	421	429	518
2) Breadth at proximal end	169	>182	131	161	>155	198
3) Length of greater expansion	172	>184	152	165	>165	205
4) Length of lesser expansion	137	?	108	135	135	166
5) Breadth of distal end	110	>119	88	101	105	140
6) Length of distal end	79	>81	59	63	71	89
7) Length of articular face (without olecranon)	412	>455	340	374	385	461

Table n°26: General data on the radii from Peirópolis.

Nº MCT-R	Site	Year	Right/Left	Notes	Morphotype
1595	Galga	1973	Left	Large	3
1598	Galga	Seventies	Right	Large	1
1610	Rodovia?	1967 or 1969	Right	Large	2
1636	Peiróp.	?	Right	Large	1
1637	Peiróp.	?	Right	Mid-size	1
1638	Peiróp.	?	Left	Mid-size	1
1648	Site 1?	1958	Left	Large	1
1649	Site 1?	1959	Left	Mid-size	2
1650	Site 1	?	Right	Smallest	1 or 2
1673	Peiróp. 1km N	?	Right	Mid-size DNPM	4
1707	São Paulo?	?	Right	Large (DNPM) Bauru deposits	3

Table nº 27: measurements of the radii from Peirópolis:
Dimensions are indicated in Fig. 16
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1595*	MCT 1598	MCT 1610	MCT 1636	MCT 1637	MCT 1638	MCT 1648*	MCT 1649	MCT 1650	MCT 1673*	MCT 1707*
1) Greatest length	> 530	451	418	478	395	396	>455	409	339	>550	~545
2) Greatest proximal diameter	?	115	113	128	98	105	>130	106	96	~160	~150
3) Least proximal diameter	?	64	84	79	69	71	?	68	59	~80	>75
4) Greatest distal diameter	?	108	119	133	107	111	?	107	85	155	?
5) Greatest distal fore and aft diameter	?	61	47	67	56	54	?	49	48	~75	?
6) Breadth about midlength	~71	~58	~51	~68	54	53	~65	52	49	~70	~65
7) Fore and aft breadth about midlength	~55	~47	~39	~52	35	37	~50	36	35	~55	~75

Table n°28: General data on the pubes from Peirópolis.

Nº MCT-R	Site	Year	Right/Left	Notes	Morphotype
1591	Galga	1972	Right		2
1592	Galga	1971	Left	"A"series? More complete proximally	2
1611	Rodovia	1969	Left	Distal fragment	?
1640	Peiróp.	?	Right		3
1641	Peiróp.	?	Left		1
1675	Peiróp.	?	Right		1
1677	Peiróp.	?	Left	Large, with closed foramen, distally broken	3
1711	Galga	1971	Right	Largest, broken in two parts	1?

Table n° 29: Measurements of the pubes from Peirópolis (in mm):
Dimensions are indicated in Fig. 17
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1591*	MCT 1592	MCT 1611*	MCT 1640	MCT 1641*	MCT 1675*	MCT 1677*	MCT 1711*
1) Total length	~460	450	>370	480	~460	~480	>510	880
2) Length from pedicel to foot	~540	530	?	522	~515	~500	>670	785
3) Length of anterior margin (curved)		540	?	549	~550	~520	?	805
4) Length posterior margin (straight)	~350	355	?	~450	~440	~380	?	?
5) Length ilium pedicel	~110	90	?	~140	~160	~150	110	285
6) Width of ilium pedicel	~65	50	?	85	75	80	100	117
7) Length of ischium pedicel	?	185	?	>145	?	?	155	?
8) Length of foot	> 150	~180	?	~190	~180	>140	?	>330

Table n°30: General data on the ischia from Peirópolis.

Nº MCT-R	Site	Year	Right/Left	Notes	Morphotype
1585	Galga	1971	Left	Pair with 1586	1
1586	Galga	1971	Right	Best preserved	1
1654	Site 1	1959	Left	Broken distally	2?
1655	Site 1	1959	Right	Well preserved	2
1661	Site 1	1959	Left	Broken blade	2
1679	Peiróp.	?	Right	Damaged	2
1689	Peiróp.	?	Right	Maybe articulates with a pelvis	3

Table n° 31: measurements of the ischia from Peirópolis (in mm).
Dimensions are indicated in Fig. 18
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1585	MCT 1586	MCT 1654*	MCT 1655	MCT 1661*	MCT 1679*	MCT 1689*
1) Distance between extremities	316	320	?	315	335	?	400
2) Length of posterior margin (curved)	364	370	?	365	388	?	457
3) Width of ischial blade (superior)	119	120	115	112	114	?	>140
4) Length of ischial blade	~120	123	~120	125	?	~100	>130
5) Width iliac pedicel (inferior)	90	95	115	?	113	?	122
6) Width of distal end	74	78	?	80	91	?	135
7) Distance "C" of Salgado et al. 1997a (inferior)	170	172	155	155	160	?	200
8) Distance "D" of Salgado et al. 1997a (superior)	369	375	>255	364	385	335	~425

Table n° 32: Evaluation of character n° 36 of SALGADO *et al.* (1997a).
C = the distance from the upper corner of the pubic blade of the ischium up to the proximal end of the iliac peduncle (7);
D = the distance from the same point up to the distal end of the posterior process (8)

Ischium	C/D ratio	Site	Character n° 36
MCT 1585	0.460	Galga	Absent
MCT 1586	0.458	Galga	"
MCT 1655	0.425	Site 1	"
MCT 1661	0.415	Site 1	"
MCT 1689	0.470	Peirópolis	"

Table n° 33: General data on the femora from Peirópolis.

N° MCT-R	Site	Year	Right/Left	Notes	Morphotype
1601	Galga	1972	Left	Smallest	1
1692	Peirópolis	?	Right		2
1693	Peirópolis?	?	Right		1
1694	Peirópolis	?	Left	Too damaged	1
1712	Peirópolis?	?	Left	Largest	1

Table n° 34: Measurements of the femora from Peirópolis (in mm):
Dimensions are indicated in Fig. 19
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1601	MCT 1692	MCT 1693	MCT 1694*	MCT 1712
1) Total length	750	875	1030	~920	1190
2) Distance of 4th trochanter from the upper margin of bone	220	310	335	-	450
3) Length of 4th trochanter	100	120	160	-	160
4) Breadth at proximal end	230	270	290	-	380
5) Length of proximal end	~90	135	>130	-	>200
6) Breadth of distal end	220	260	320	-	350
7) Length of tibial condyle	>120	195	>140	-	290
8) Length fibular condyle	~140	~160	190	-	260
9) Width of shaft	~110	~180	~190	-	160

Table n°35: General data on the tibiae from Peirópolis.

N° MCT-R	Site	Year	Right/Left	Notes	Morphotype
1587	Galga	1972	Left	Fragmented	1
1681	Peiróp.	?	Right	Small	1
1683	Peiróp.	?	Right	Large	1
1695	Galga? (DAC)	1967	Right	Large, DNPM	1

Table n° 36: measurements of the tibiae from Peirópolis (in mm):
Dimensions are indicated in Fig. 20
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1587*	MCT 1681	MCT 1683*	MCT 1695
1) Total length (internal)	~450	475	750	755
2) Total length (extern.)	445	460	730	~720
3) Width at middle	~78	85	140	145
4) Minimum width	~75	73	115	110
5) Distance of minimum width from upper margin	~270	295	520	480
6) Cnemial crest – upper length	105	95	?	140
7) Cnemial crest – lower length	~120	~140	>190	140
8) Cnemial crest– length	60	60	>90	105
9) Proximal width	~130	133	245	~190
10) Proximal breadth	~105	114	150	~100
11) Breadth of distal end	143	145	225	>160
12) Width of distal end	~90	95	165	~140

Table n°37: General data on the fibulae from Peirópolis.

N° MCT-R	Site	Year	Right/Left	Notes	Morphotype
1588	Galga	1972	Left	Smallest slender	1
1607	Rodovia	1967	Right	Large, lacks distal end	2
1608	Rodovia	1967	Right	Large	2
1657	Site 1	1959	Left	Slender	1
1660	Site 1	1959	Right	Slender	1
1696	Galga	1967	Left	DNPM – largest	2

Table n° 38: measurements of the fibulae from Peirópolis (in mm):
Dimensions are indicated in Fig. 21
* indicates incomplete bones
~ indicates estimated measurement; > indicates measurement of the preserved part

Dimensions	MCT 1588	MCT 1607*	MCT 1608	MCT 1657*	MCT 1660	MCT 1696
1) Total length	430	>415 preserved part	542	486	478	725
2) Breadth of proximal end	57	65	> 75	~60	60	110
3) Lateral width proximal	130	134	160	~125	125	198
4) Breadth at distal end	67	?	105	>50	82	128
5) Width distal end	90	?	100	~95	90	156
6) Width at the middle	54	~58	~70	~52	~52	~77
7) Width of stalk without crest	106	102	130	~105	116	168

Table n°39: number of Morphotypes for each bone category:

Category	Morphotype
Scapula	1 and 2
Coracoid	1
Sternal plate	1 and 2
Humerus	1
Ulna	1 and 2
Radius	1, 2, 3 and 4
Pubis	1, 2, 3
Ischium	1, 2, 3
Femur	1 and 2
Tibia	1
Fibula	1 and 2

Table n°40: Distribution of morphotypes by each site.

Category	Galga	Rodovia	Site 1	Peirópolis (surroundings)
Scapula	2	-	2	1 and 2
Coracoid	1	-	1	1
Sternal plate	1	2?	1 and 2	-
Humerus	1	-	1	1
Ulna	-	2	1 and 2?	1 and 2
Radius	1 and 3	2	1 and 2	1, 3 and 4
Pubis	2 and 1?	-	-	1 and 3
Ischium	1	-	1/2? e 2	2 and 3
Femur	1	-	-	1 and 2
Tibia	1	-	-	1
Fibula	1 e 2	2	1	-

ILLUSTRATIONS

Fig 1. Llewellyn Ivor Price, the Palaeontologist who has unearthed the Peirópolis bones.

Fig 2. Map of Brazil, showing the locality of Peirópolis, where the bones have been found. (Modified from Campos & Kellner, 1991).

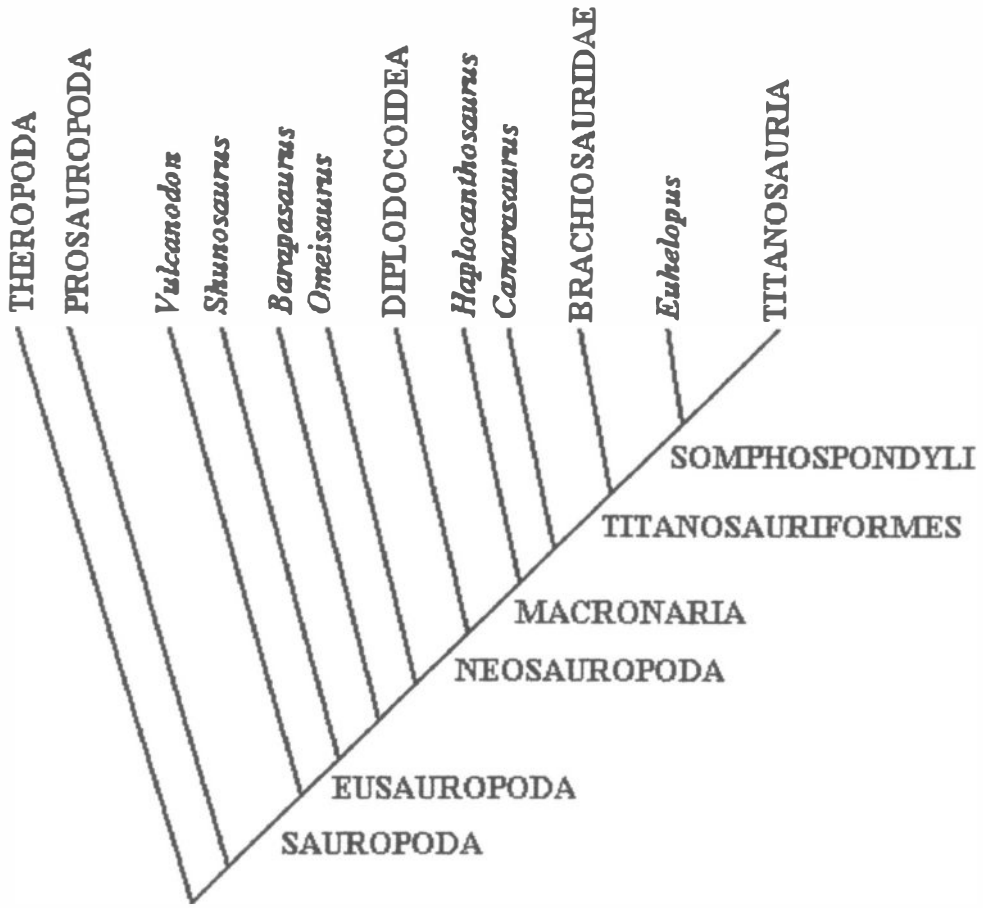


Fig. 3. Cladogram depicting the relationships of the Sauropoda (after Wilson & Sereno, 1998).

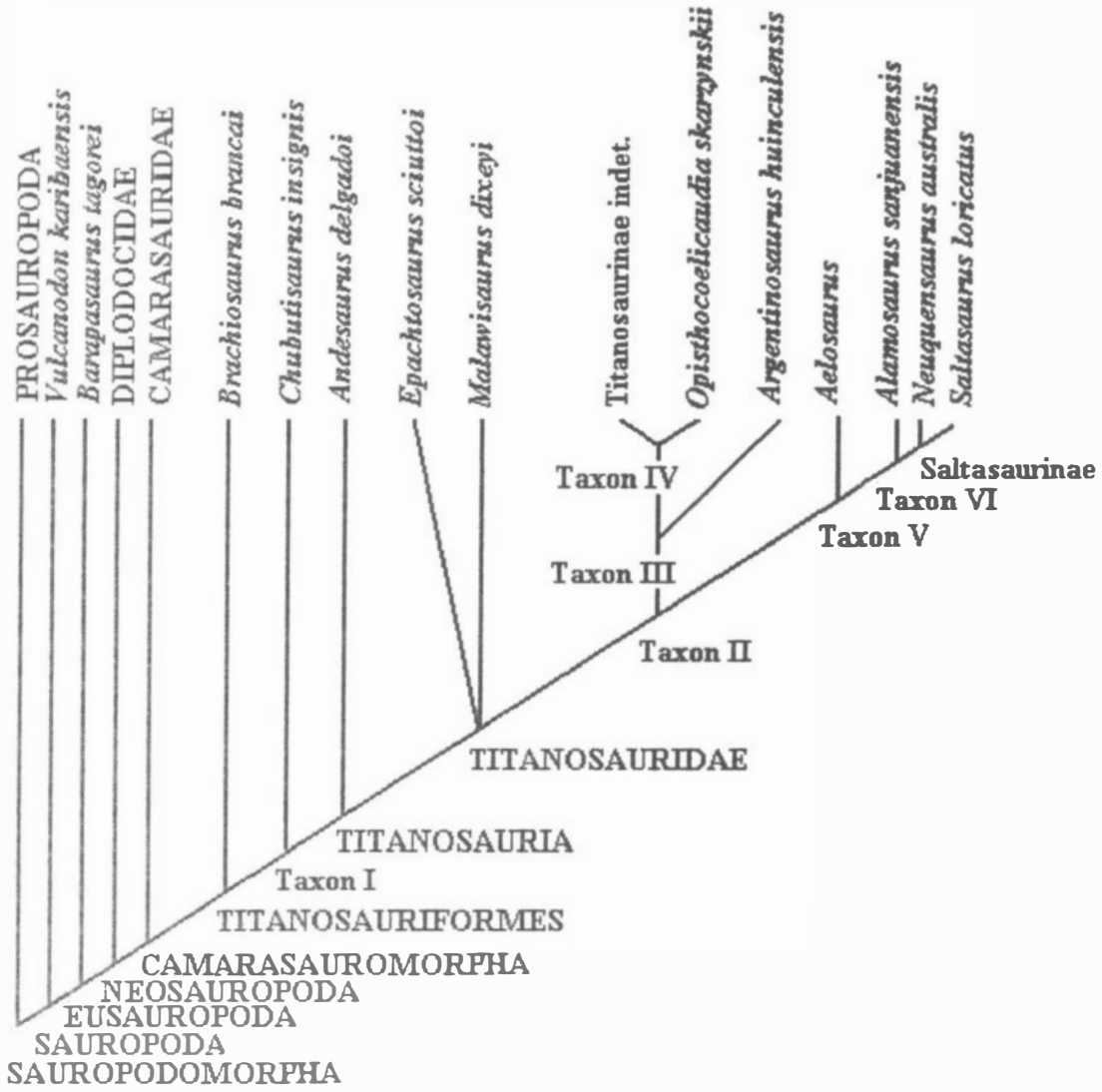


Fig. 4. Cladogram depicting the relationships of the Sauropodomorpha (after Salgado *et al.*, 1997).

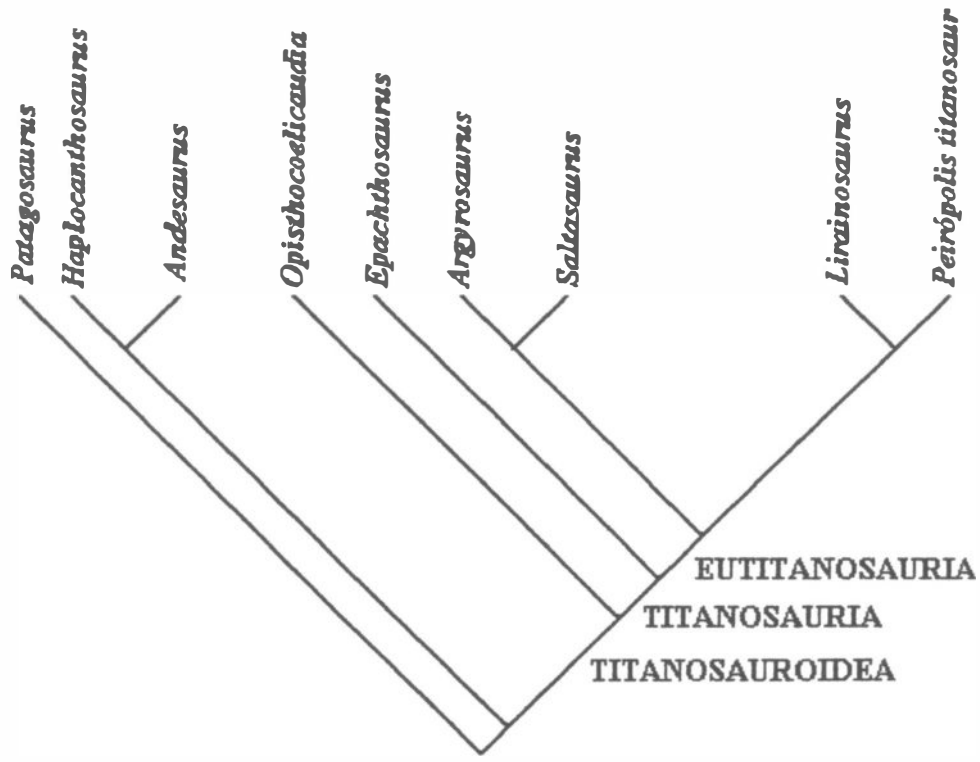


Fig. 5. Cladogram depicting the relationships of the Sauropoda (after Sanz *et al.*, 1999).

Fig. 6. Field map of Site 1 (After Campos & Kellner, 1999).

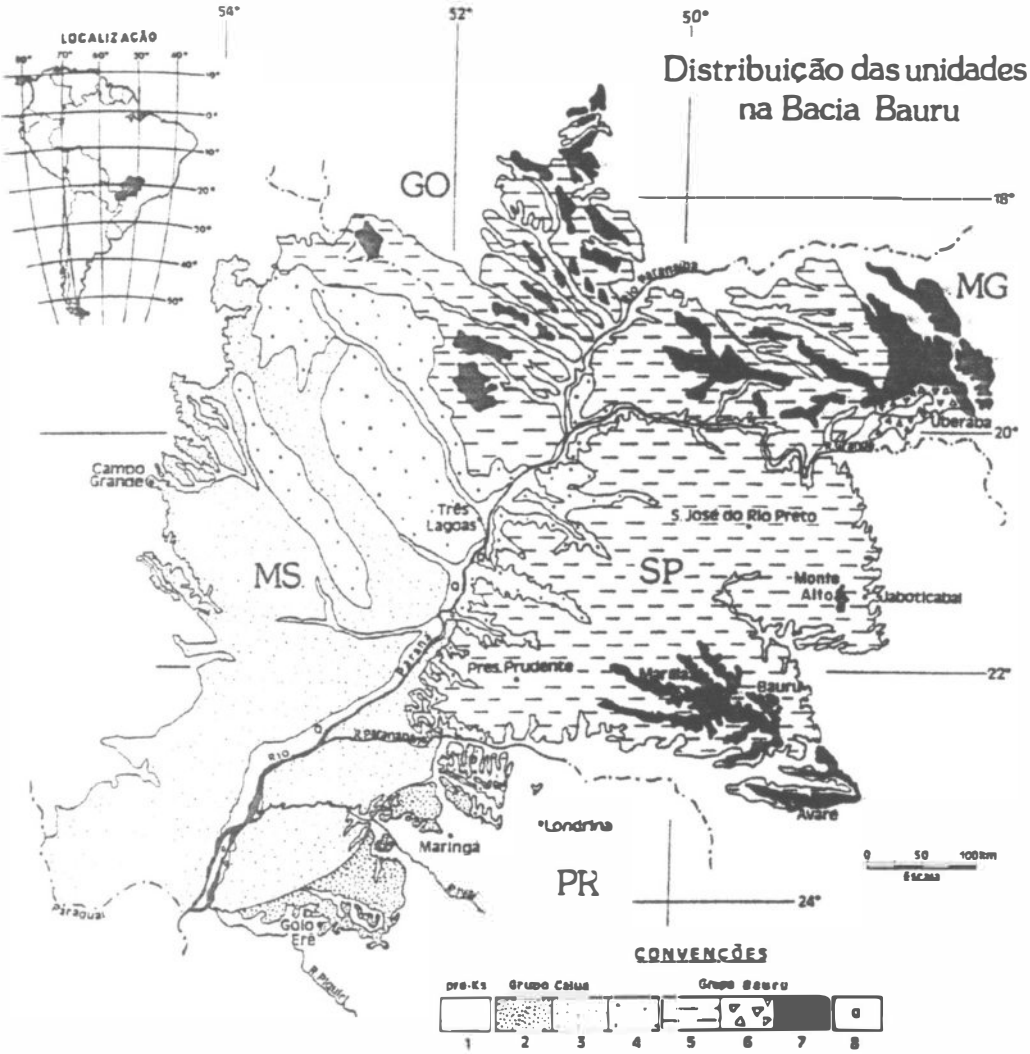


Fig. 7. Bauru Basin, the sedimentary area from where the bones have been extracted. 1. Basal pre-Cretacic rocks; 2. Goio Erê Formation. 3. Rio Paraná Formation; 4. Santo Anastácio Formation; 5. Adamantina Formation; 6. Uberaba Formation; 7. Marília Formation; 8. Quaternary deposits. (After Fernandes & Coimbra, 1996).

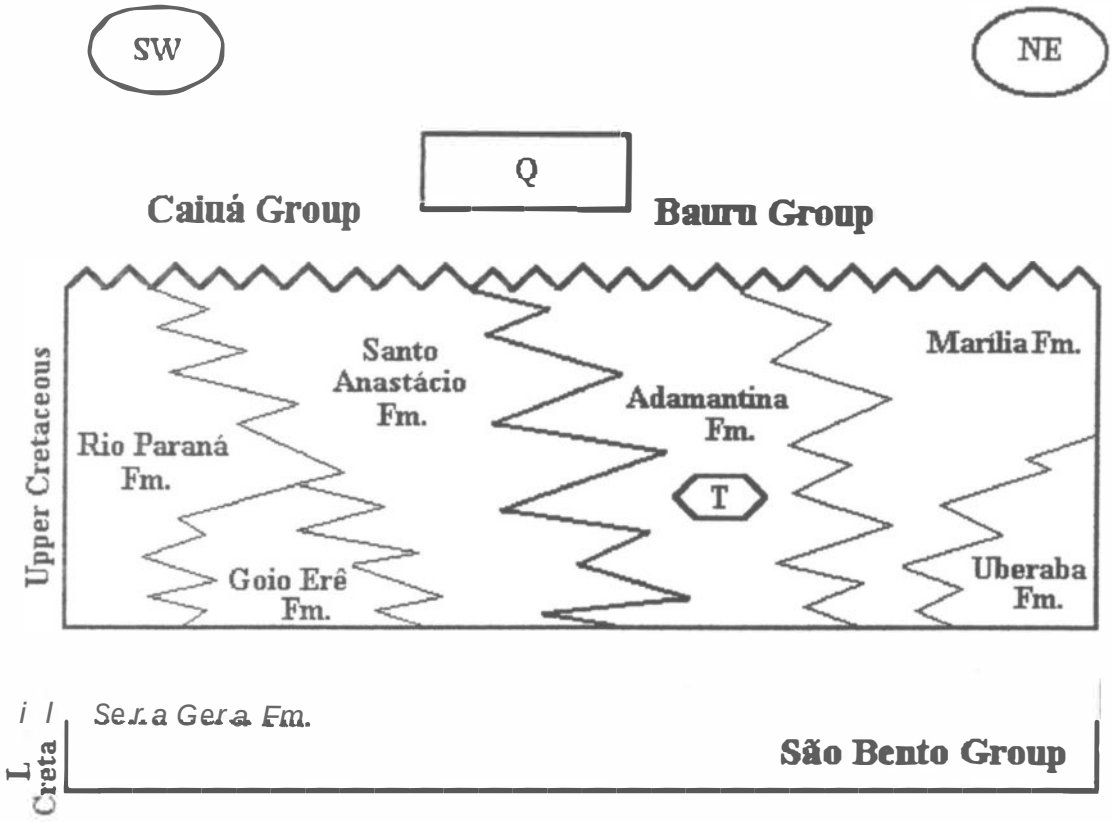


Fig. 8. Stratigraphic profile of the Bauru Group. Q. quaternary aluvial deposits; T. Taiúva analcimites. (Modified from Fernandes & Coimbra, 1996).

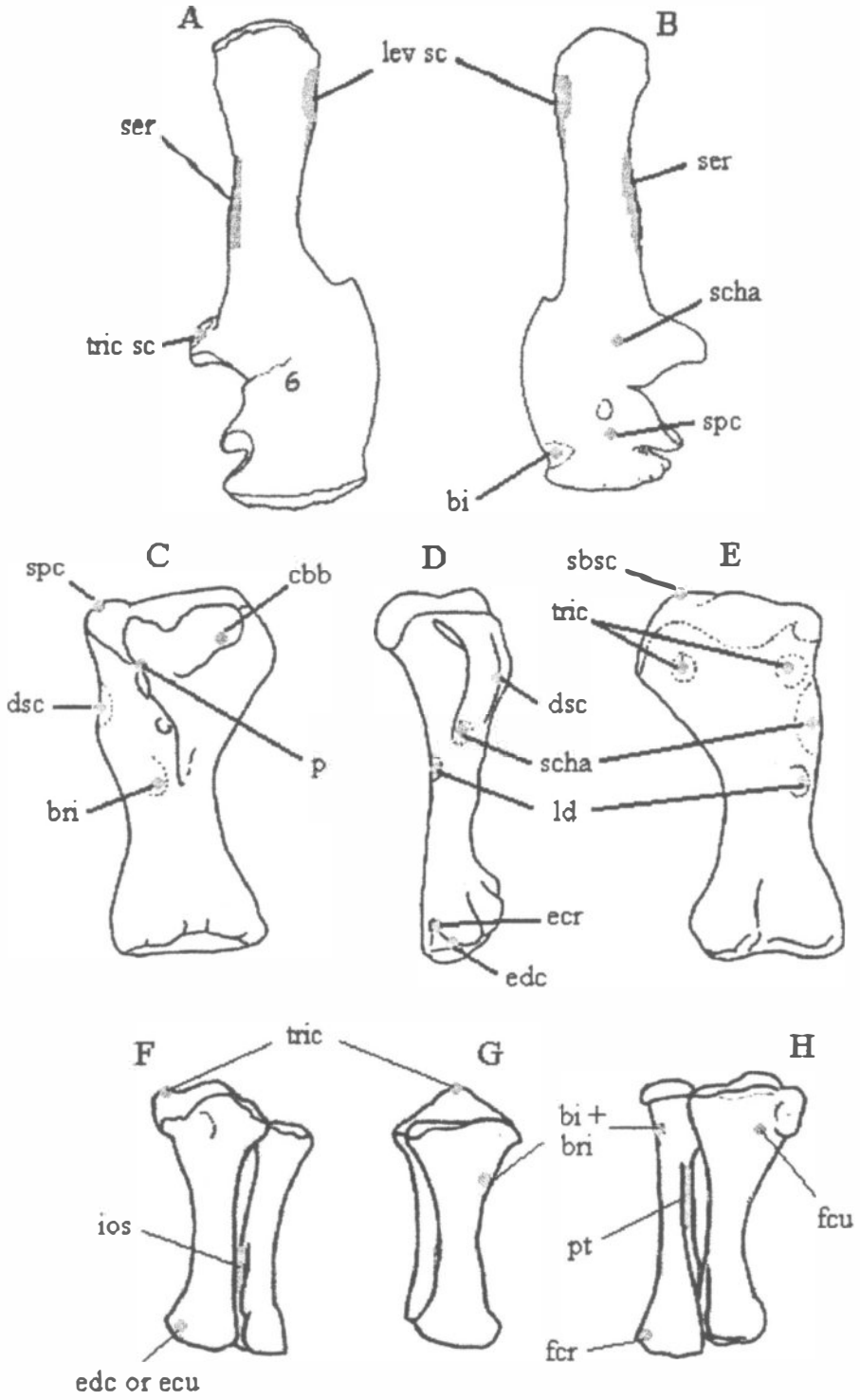


Fig. 9. Principal muscles of the anterior limb, as discussed in the in the text (modified from Borsuk-Bialynicka, 1977). Left scapula in: A) medial and B) lateral views. Right humerus in: C) anterior, D) lateral and E) posterior views. Right ulna and radius in: F) lateral, G) anterior and H) medial views. See following page for abbreviations.

Nomenclature and abbreviations:

Abbreviation	Muscle
Bi	*Biceps*
Bri	*Brachialis inferior*
Cbb	*Coracobrachialis brevis*
Dsc	*Scapulas deltoid*
Ecr	*Extensor carpi radialis*
Ecu	*Extensor carpi ulnaris*
Edc	*Extensor digiturom communis*
Fcr	*Flexor carpi radialis*
Fcu	*Flexor carpi ulnaris*
Ios	*Interosseus*
Ld	*Latissimus dorsi*
Lev sc	*Levator scapulae*
P	*Pectoralis*
Pt	*Pronator teres*
Sbsc	*Subcoracoscapularis*
Scha	*Scapulohumeralis anterior*
Ser	*Serratus*
Spc	*Supracoracoideus*
Tri	*Triceps*
Tric sc	*Triceps head of scapula*

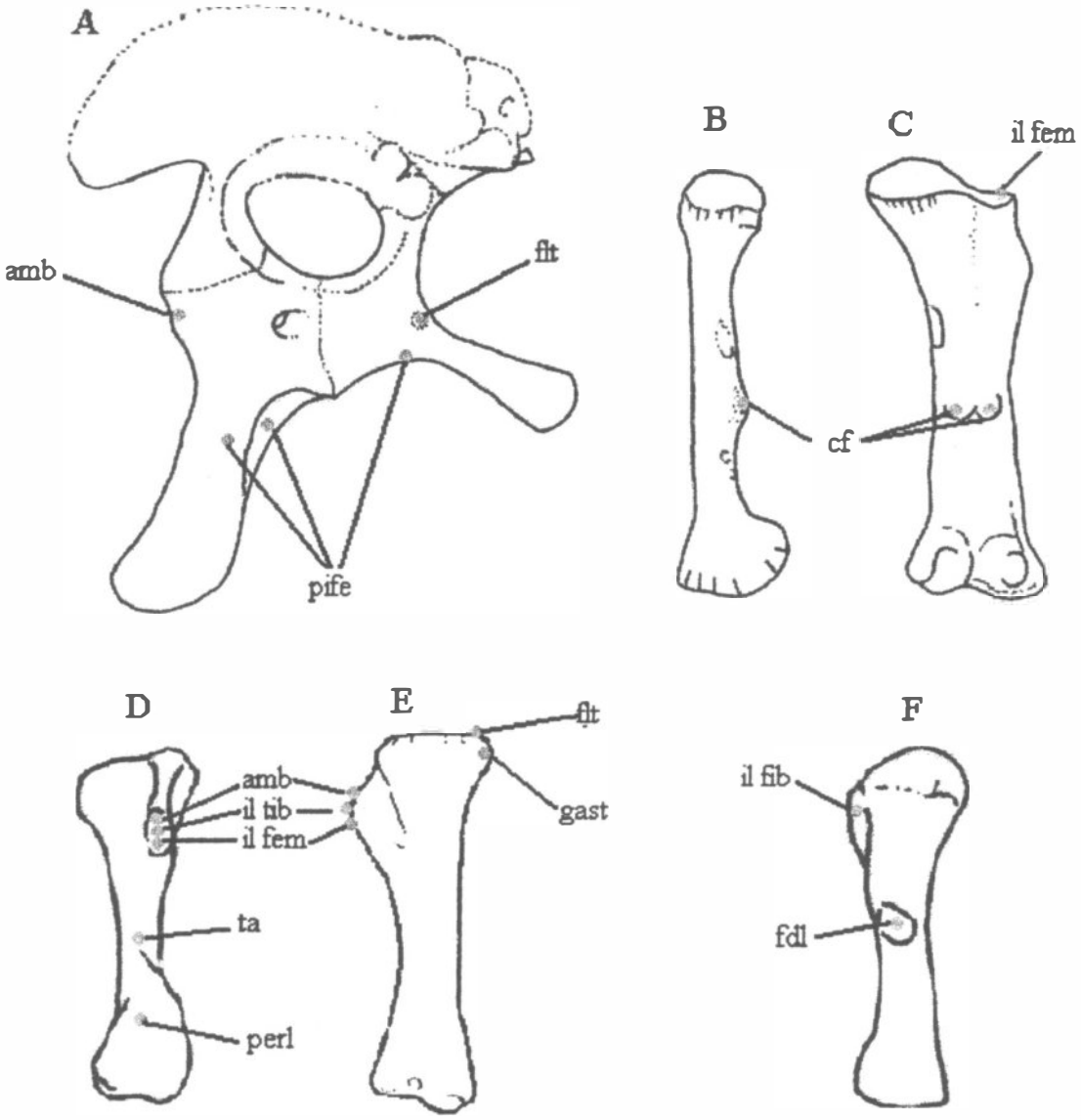


Fig. 10. Principal muscles of the posterior limb, as discussed in the in the text (modified from Borsuk-Bialynicka, 1977). A) Left pubis and ischium in lateral view. right femur in: B) medial and C) posterior views. Right tibia in D) anterior and E) lateral views. F) right fibula in lateral view. See following page for abbreviations.

Nomenclature and abbreviations:

Abbreviation	Muscle
Amb	*Ambiens*
Cf	*Caudifemoralis*
Fdl	*Flexor digitorum longus*
Flt	*Flexor tibialis*
Gast	*Gastrocnemius*
Il fem	*Iliofemoralis*
Il fib	*Iliofibularis*
Il tib	*Iliotibialis*
Perl	*Peroneus longus*
Pife	*Puboischiofemoralis externus*
Ta	*Tibialis anterior*

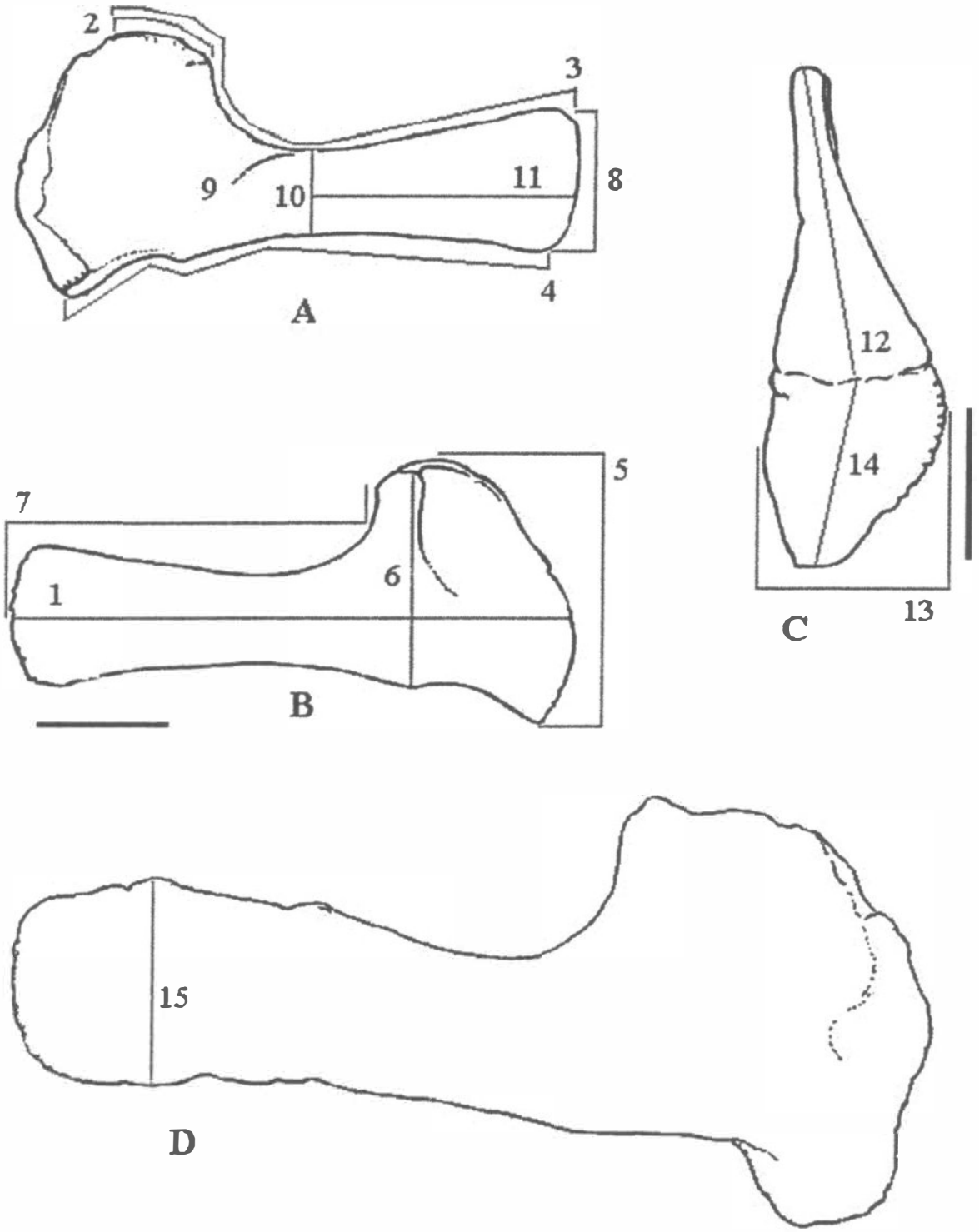


Fig. 11. Right scapula in: A) medial, B) lateral, C) proximal views; D) distal blade, showing expansion. Scale bar equals 10 cm. D) is not to scale.

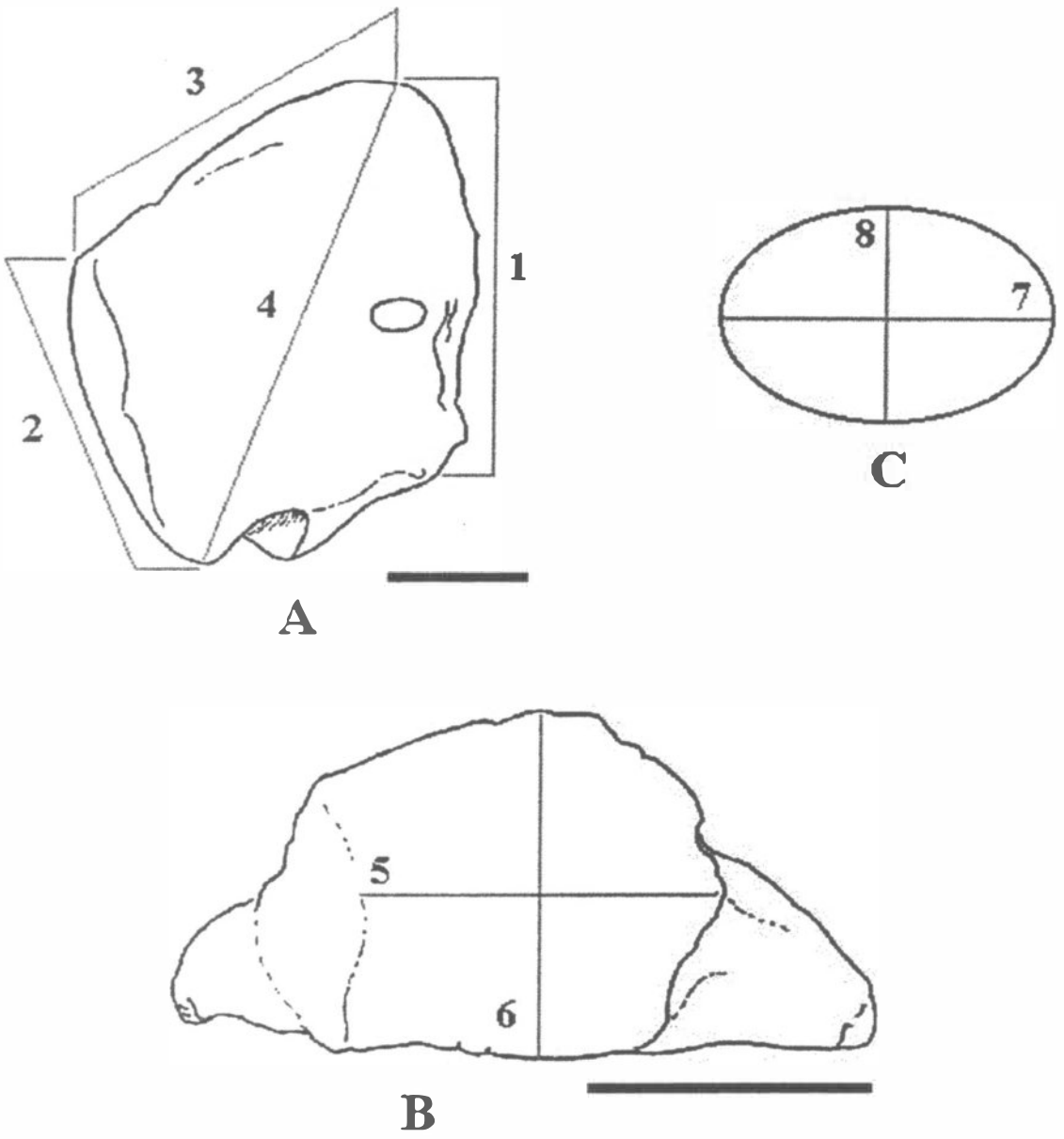


Fig. 12. Right coracoid in: A) medial, B) posterior views; C) coracoidal foramen. Scale bar equals 10 cm. C) is not to scale.

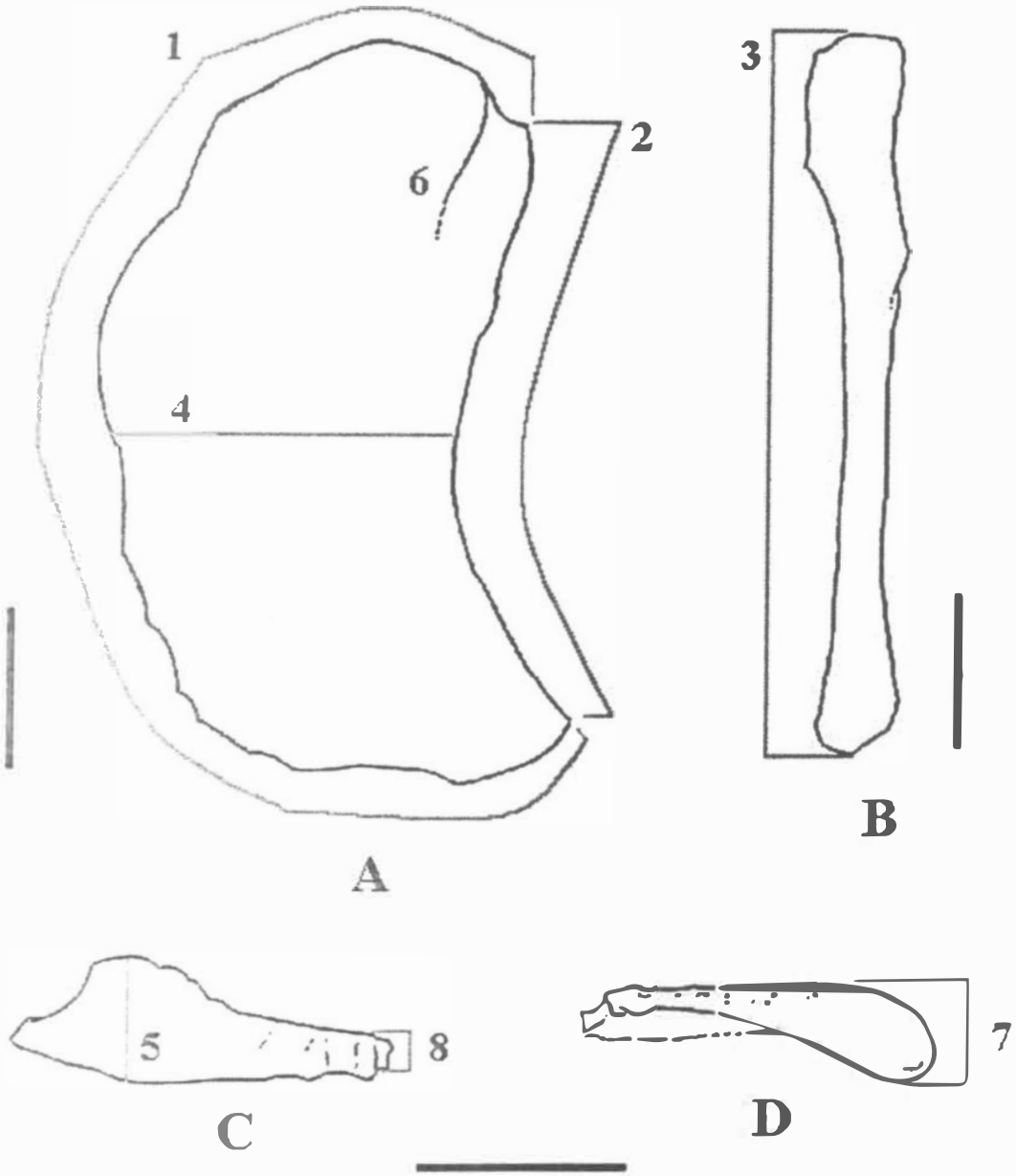


Fig. 13. Left sternal plate in: A) ventral, B) lateral, C) proximal, D) distal views. Scale bar equals 10 cm.

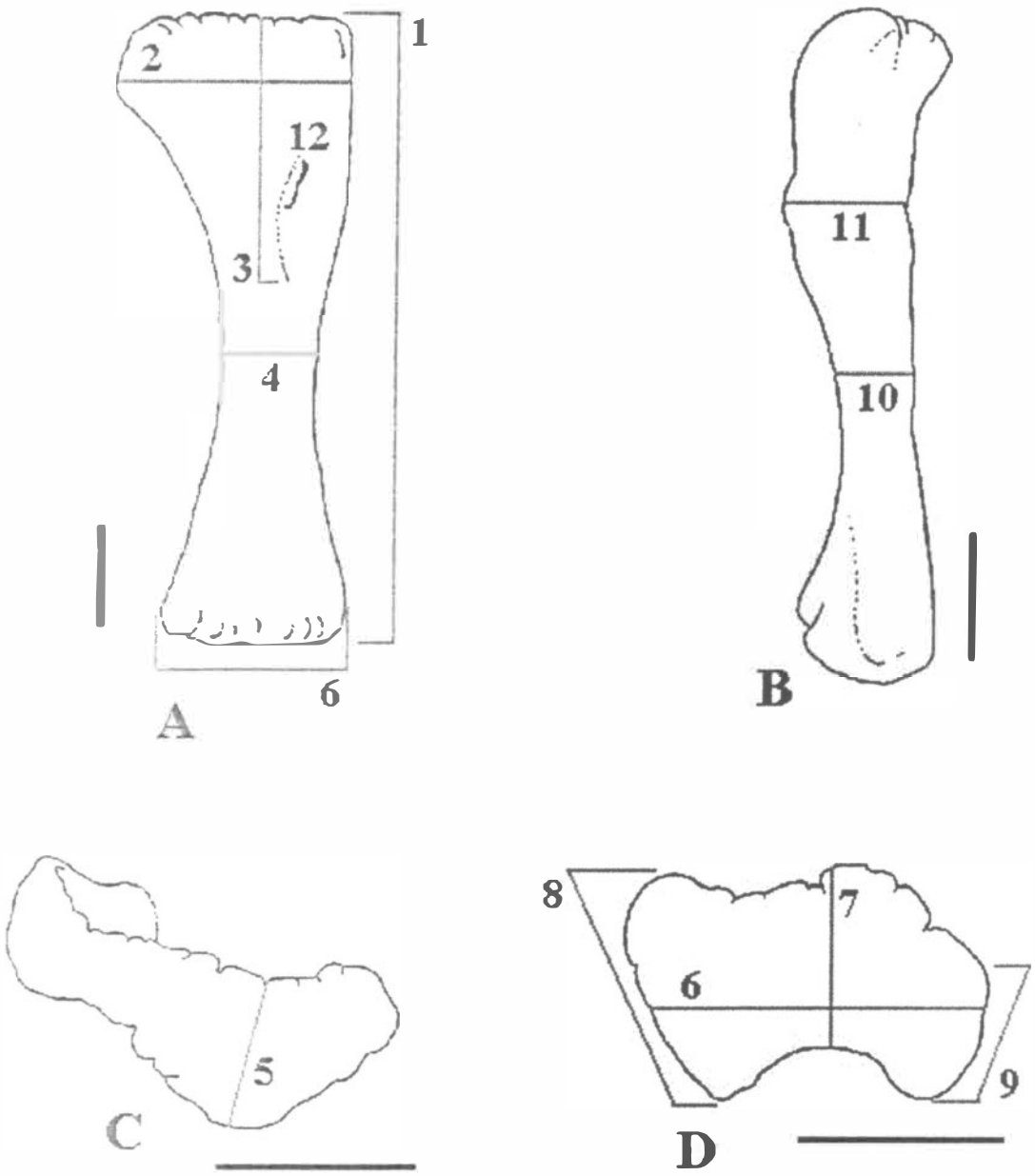


Fig. 14. Left humerus in: A) anterior, B) lateral, C) proximal and D) distal views, showing the measurements. Scale bar equals 10 cm.

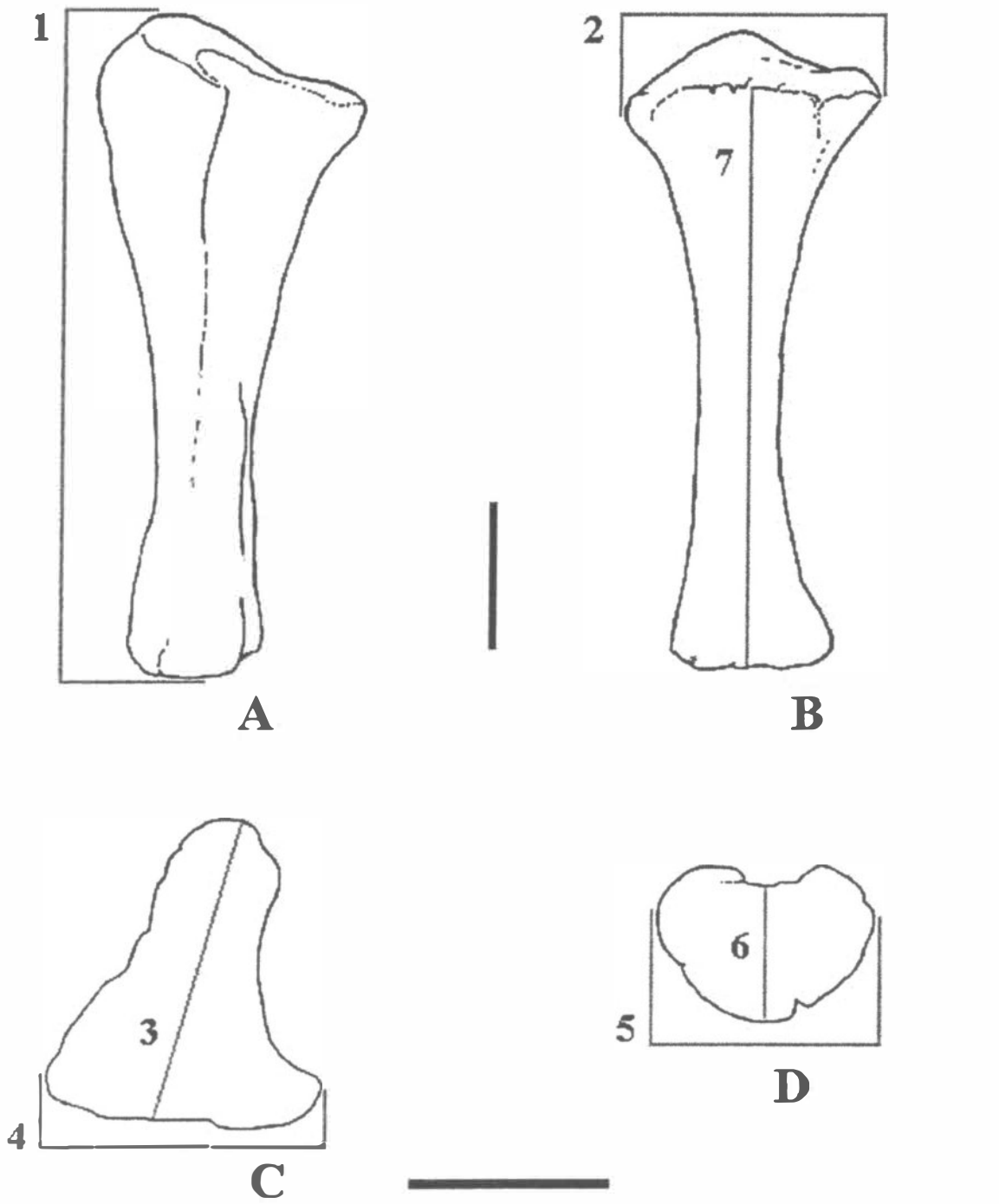


Fig. 15: Right ulna in: A) lateral, B) radial, C) proximal, D) distal views, showing the measurements. Scale bar equals 10 cm.

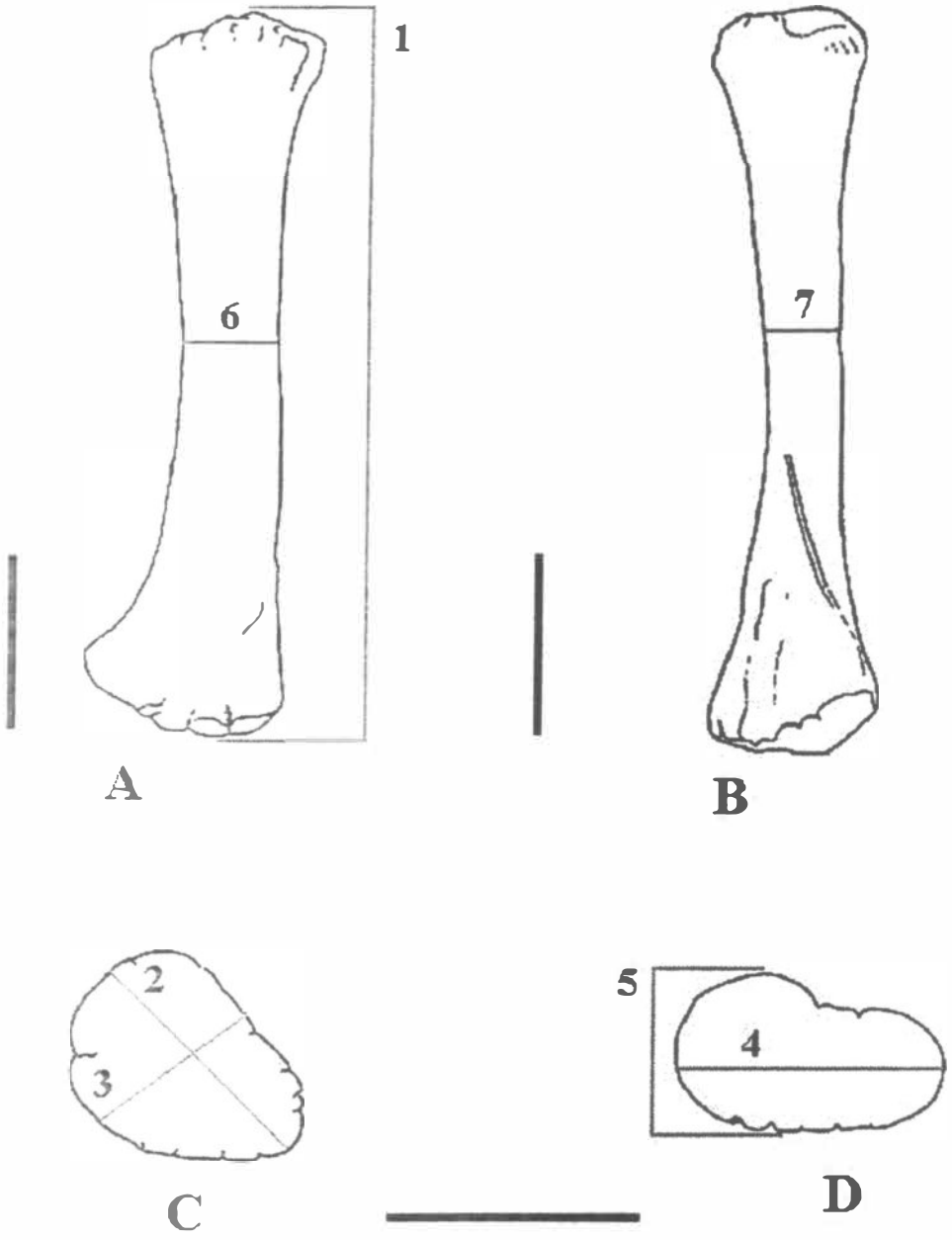


Fig. 16. Right radius in: A) anterior, B) lateral, C) proximal, D) distal views, showing the measurements. Scale bar equals 10 cm.

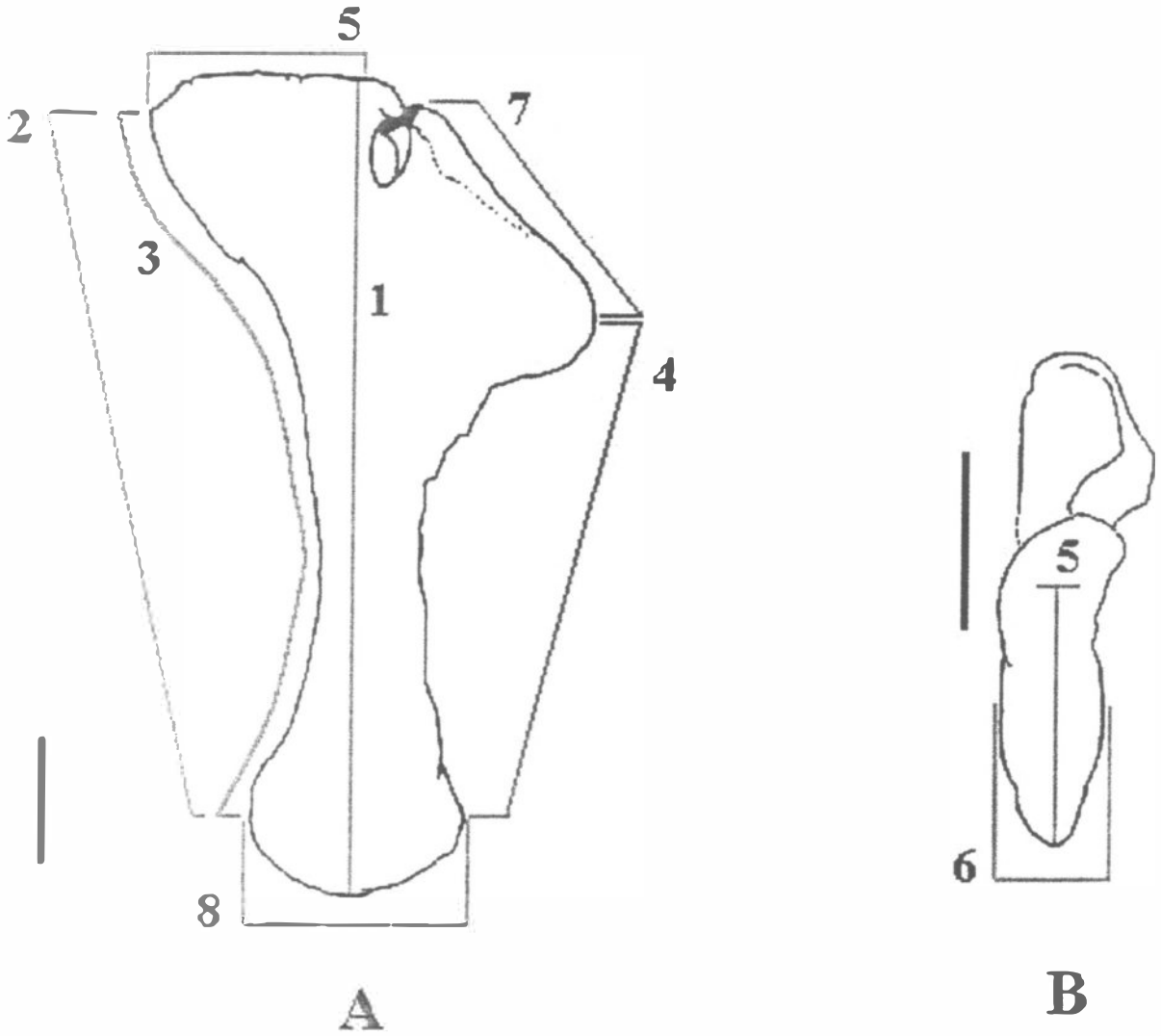


Fig. 17. Left pubis in A) lateral and B) proximal views, showing the measurements. Scale bar equals 10 cm.

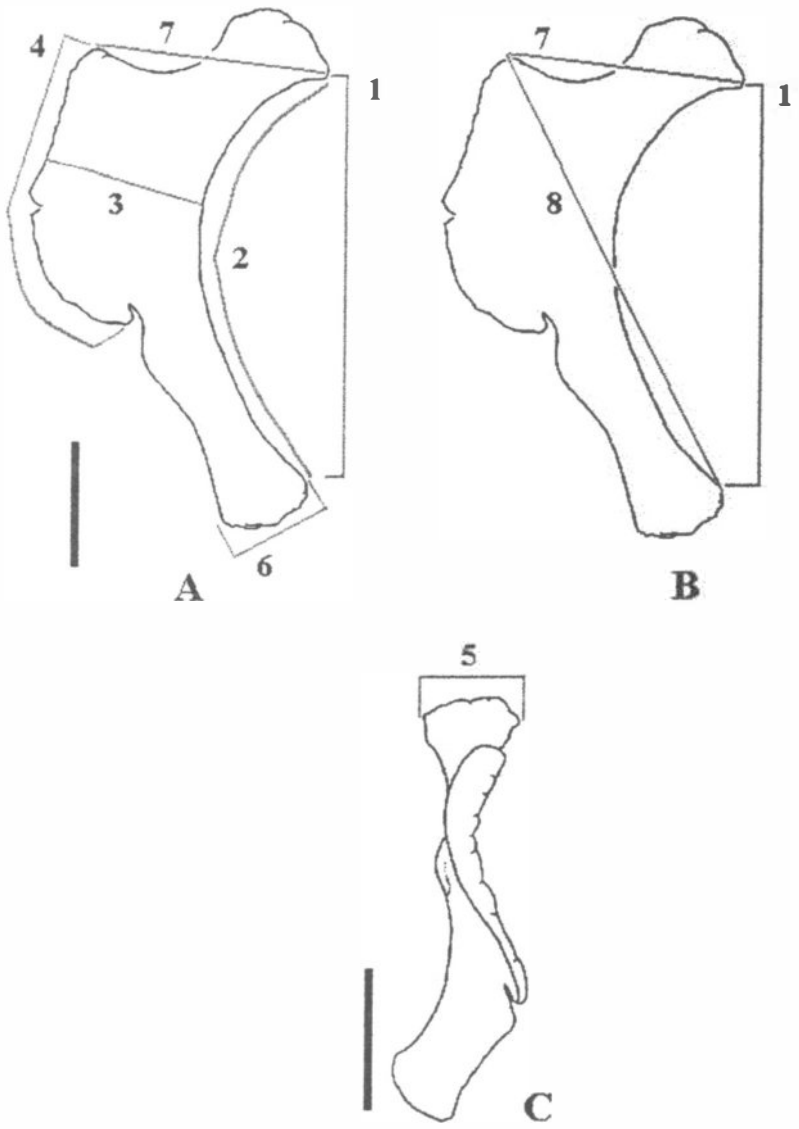


Fig. 18. Right ischium in: A) superior, B) superior and C) anterior views, showing the measurements. Scale bar equals 10 cm.

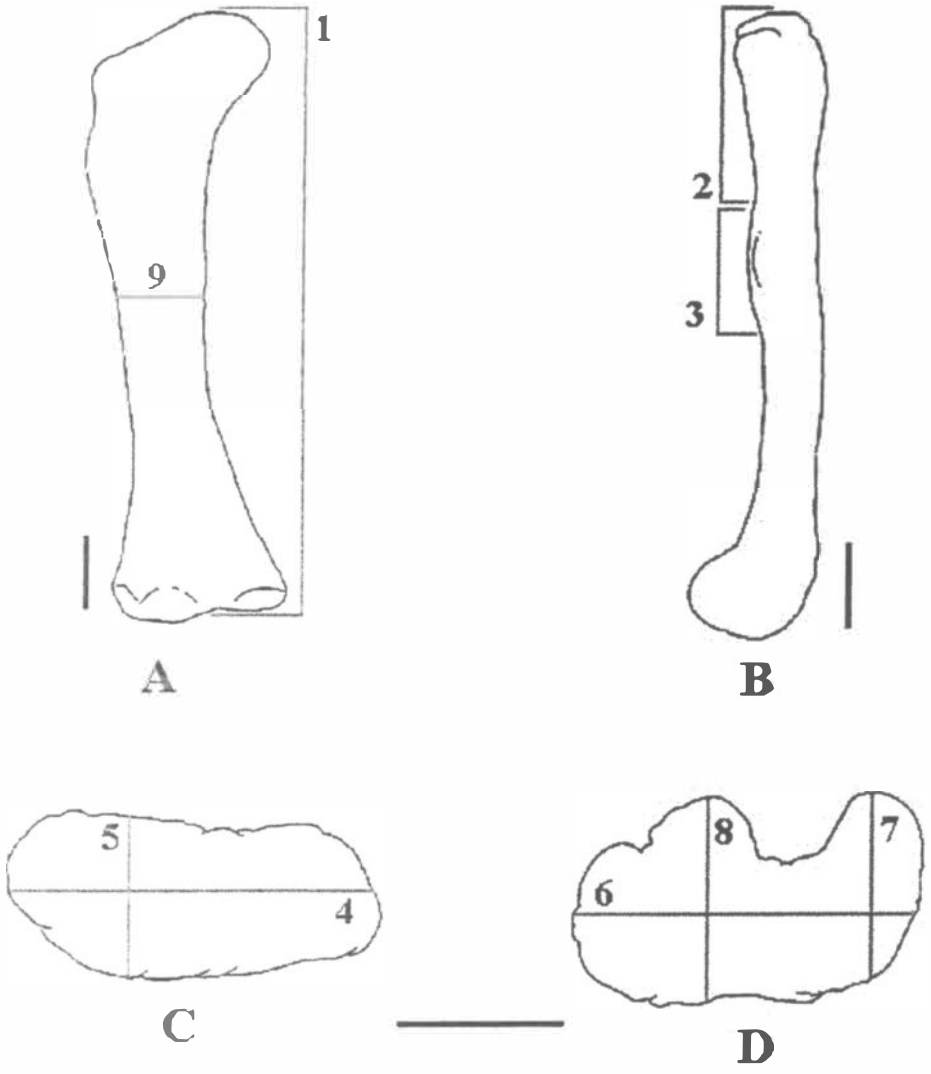


Fig. 19. Left femur in: A) posterior, B) medial, C) proximal and D) distal views, showing the measurements. Scale bar equals 10 cm.

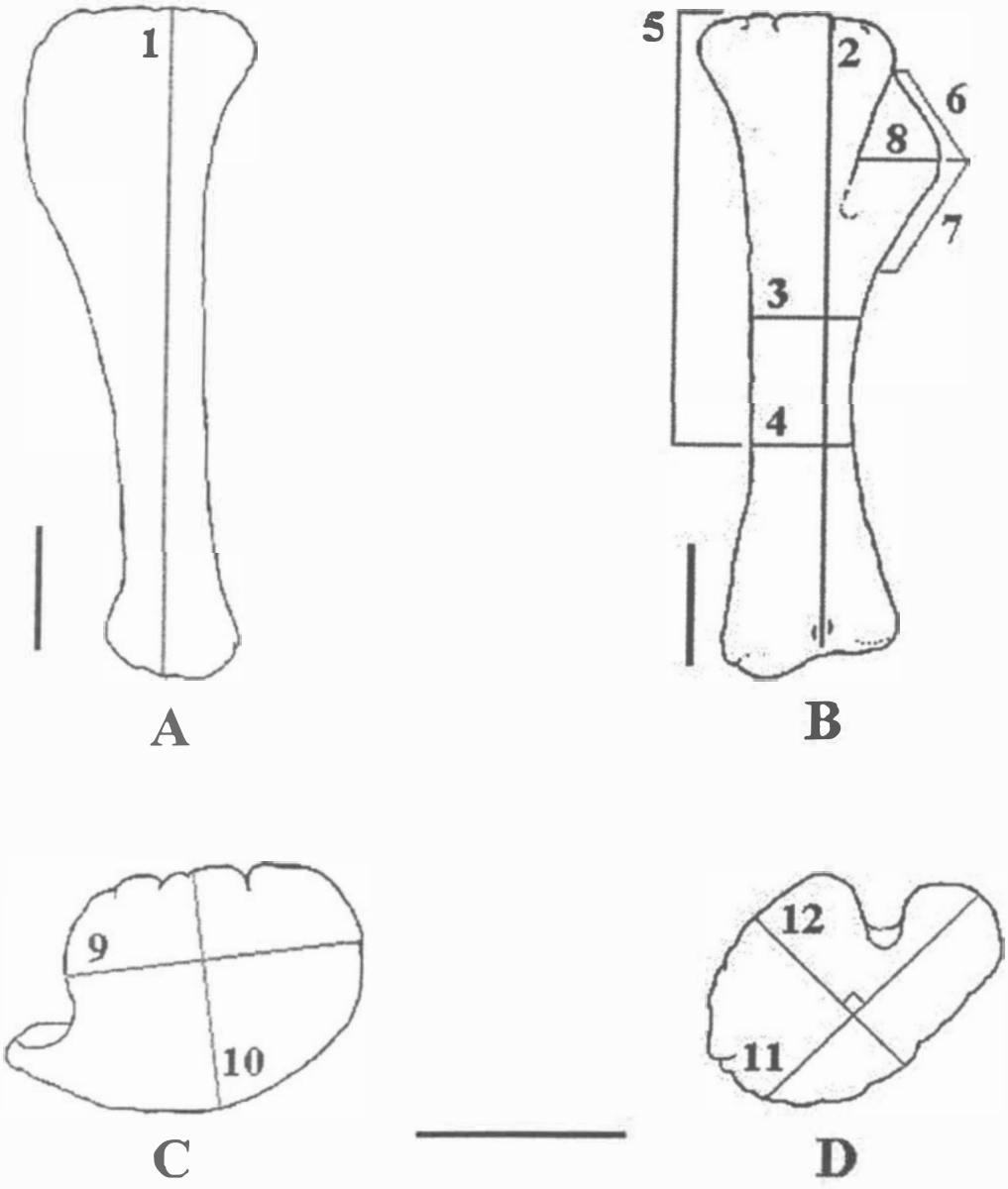


Fig. 20. Right tibia in: A) medial, B) lateral, C) proximal and D) distal views, showing the measurements. Scale bar equals 10 cm.

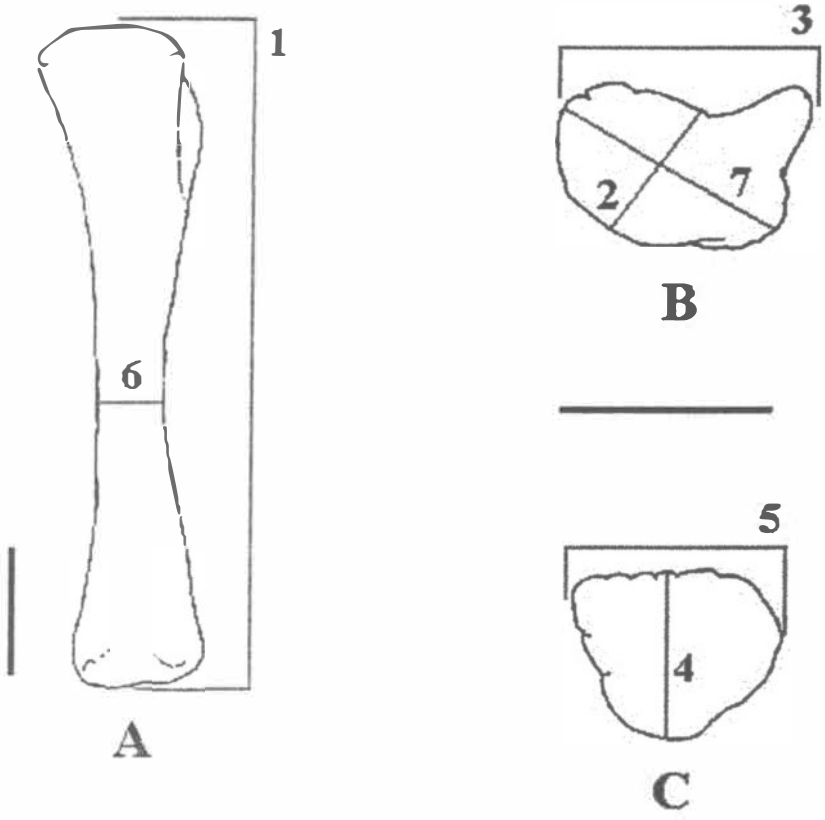


Fig. 21. Right fibula in A) lateral, B) proximal and C) distal views, showing the measurements. Scale bar equals 10 cm.

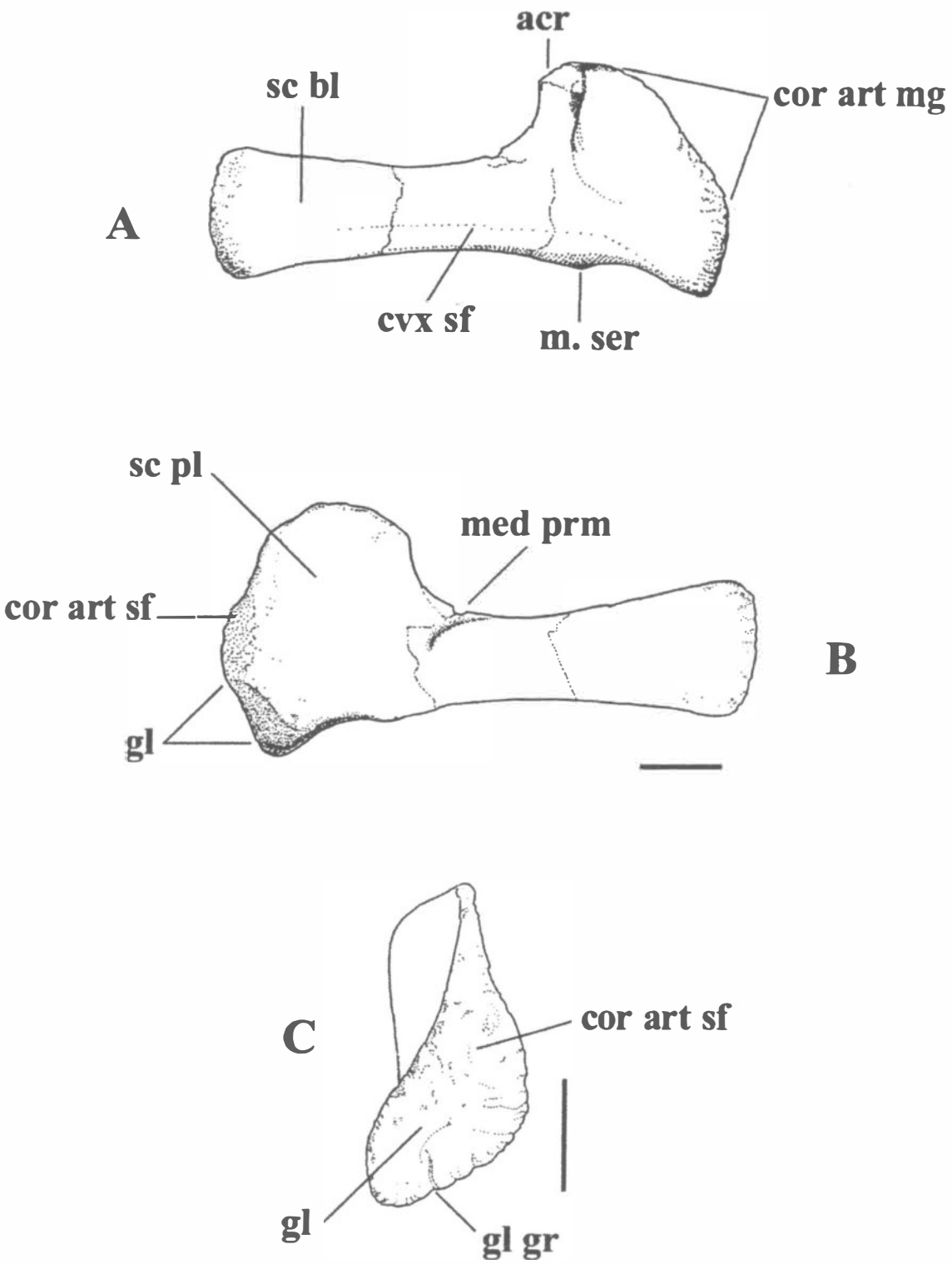
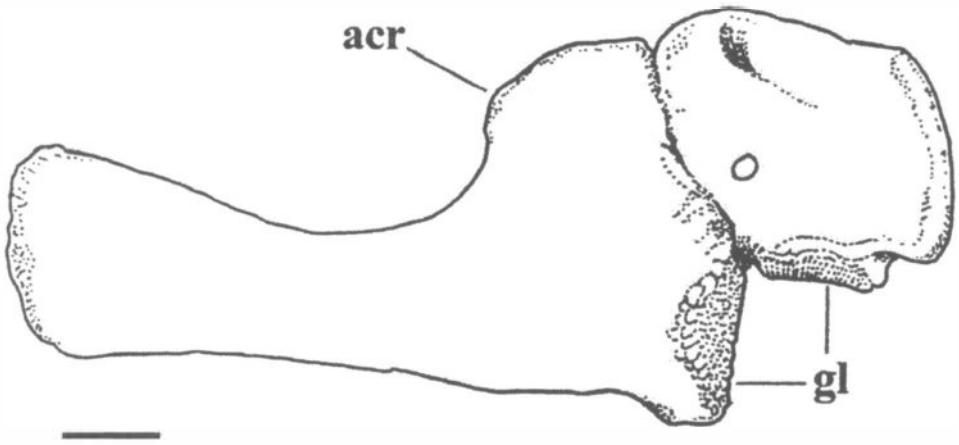
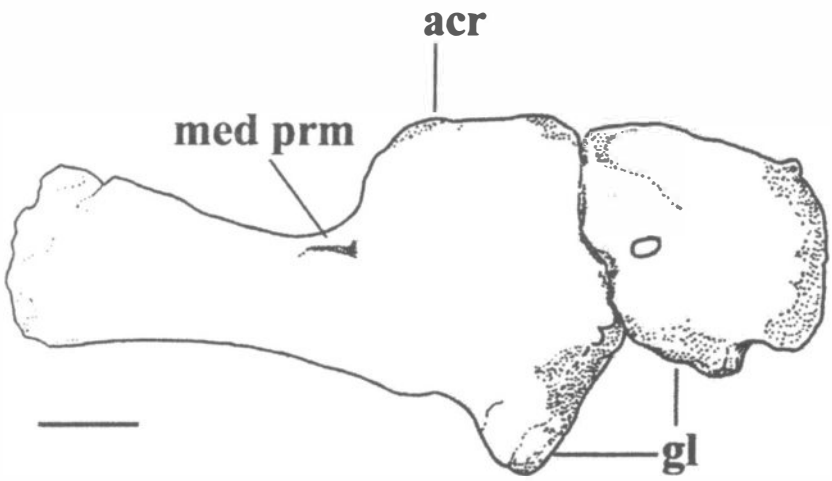


Fig. 22. Right scapula MCT 1680-R in: A) lateral; B) medial and C) glenoidal views.
(acr) acromion, (co art mg) coracoidal articular margin, (co art sf) coracoidal articular surface, (cvx sf) convex surface of blade, (gl) glenoid, (gl gr) glenoidal groove, (m.ser) muscle scar for m. serratus, (med prm) medial prominence, (sc bl) scapular blade, (sc pl) scapular plate. Scale bar equals 10 cm.

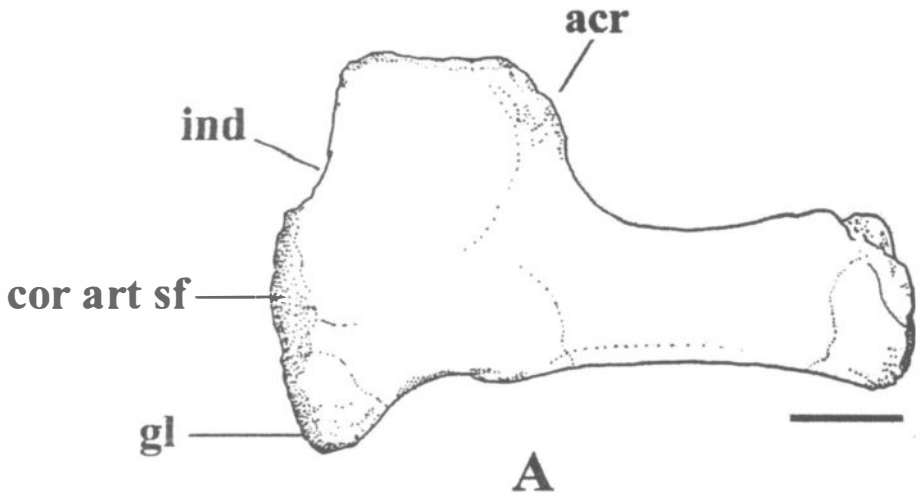


A



B

Fig. 23. Left scapulae with articulated coracoids, in medial view. A) MCT 1703-R, B) MCT 1691-R (ind) indentation, (med prm) medial prominence. Scale bar equals 10 cm.



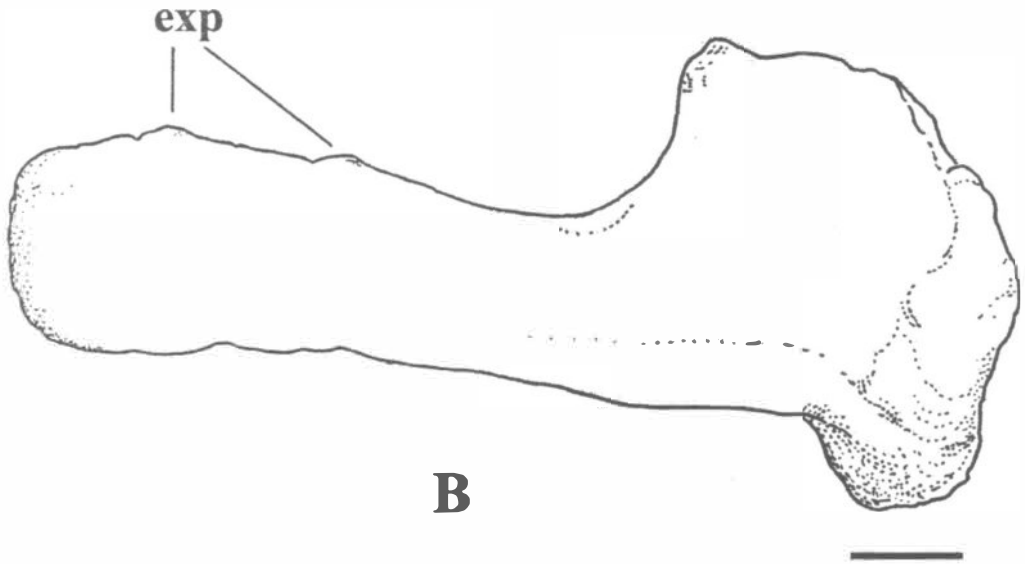


Fig. 24. Left scapulae A) MCT 1691-R without coracoid, in lateral view. B) MCT 1709-R in medial view. (exp) upper expansion of blade, (ind) indentation. Scale bar equals 10 cm.

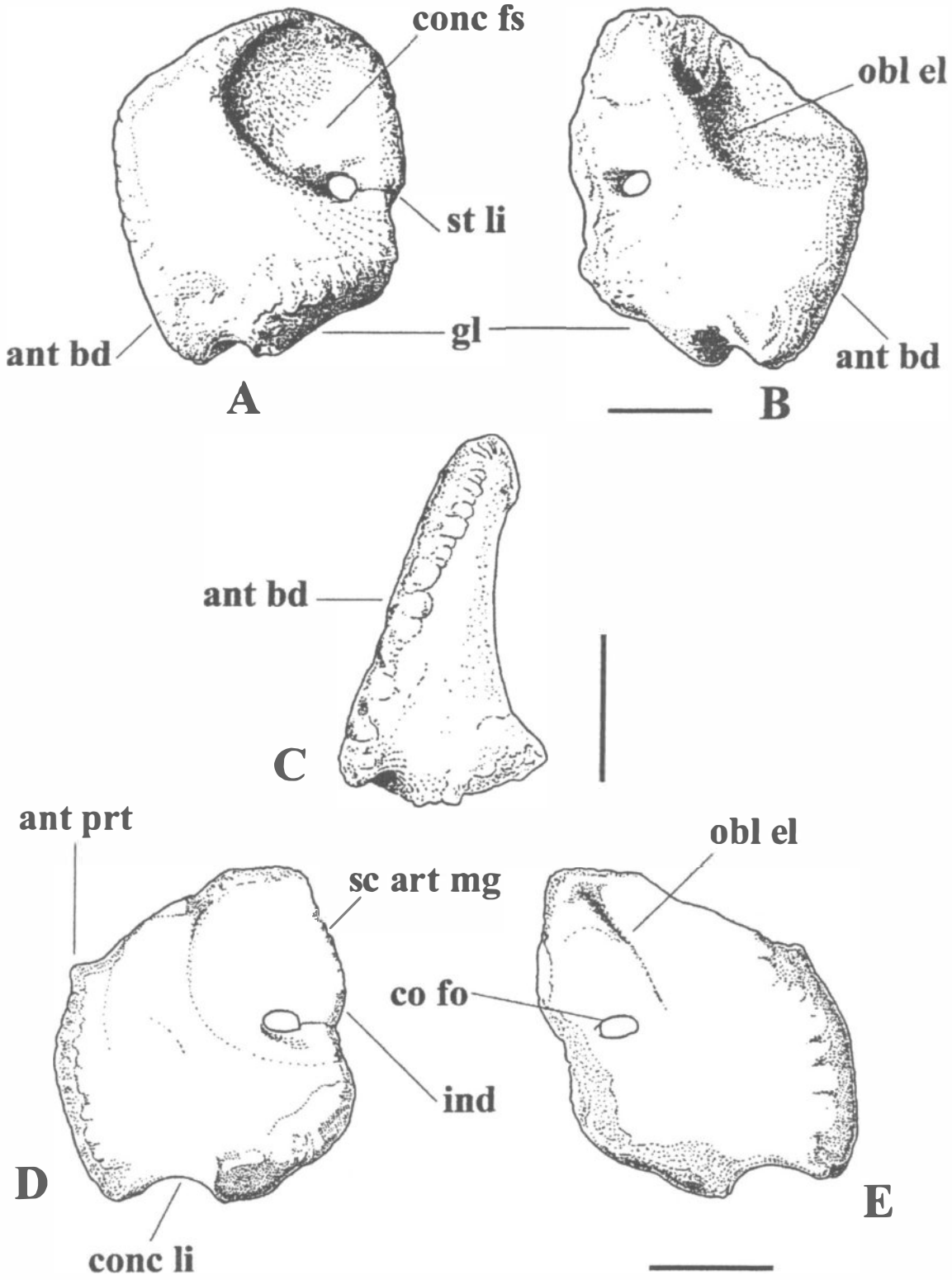


Fig. 25. Left coracoids MCT 1703-R in: A) lateral, B) medial and C) anterior views and MCT 1691-R in D) lateral and E) medial views. (ant bd) anteromedial border, (ant prt) anterior protuberance, (conc li) concave curved line, (conc fs) concave fossa), (cor fo) coracoidal foramen, (gl) glenoid), (ind) indentation, (obl el) oblique elevation, (sc art mg) scapualr articular margin, (sut li) suture line. Scale bar equals 10 cm.

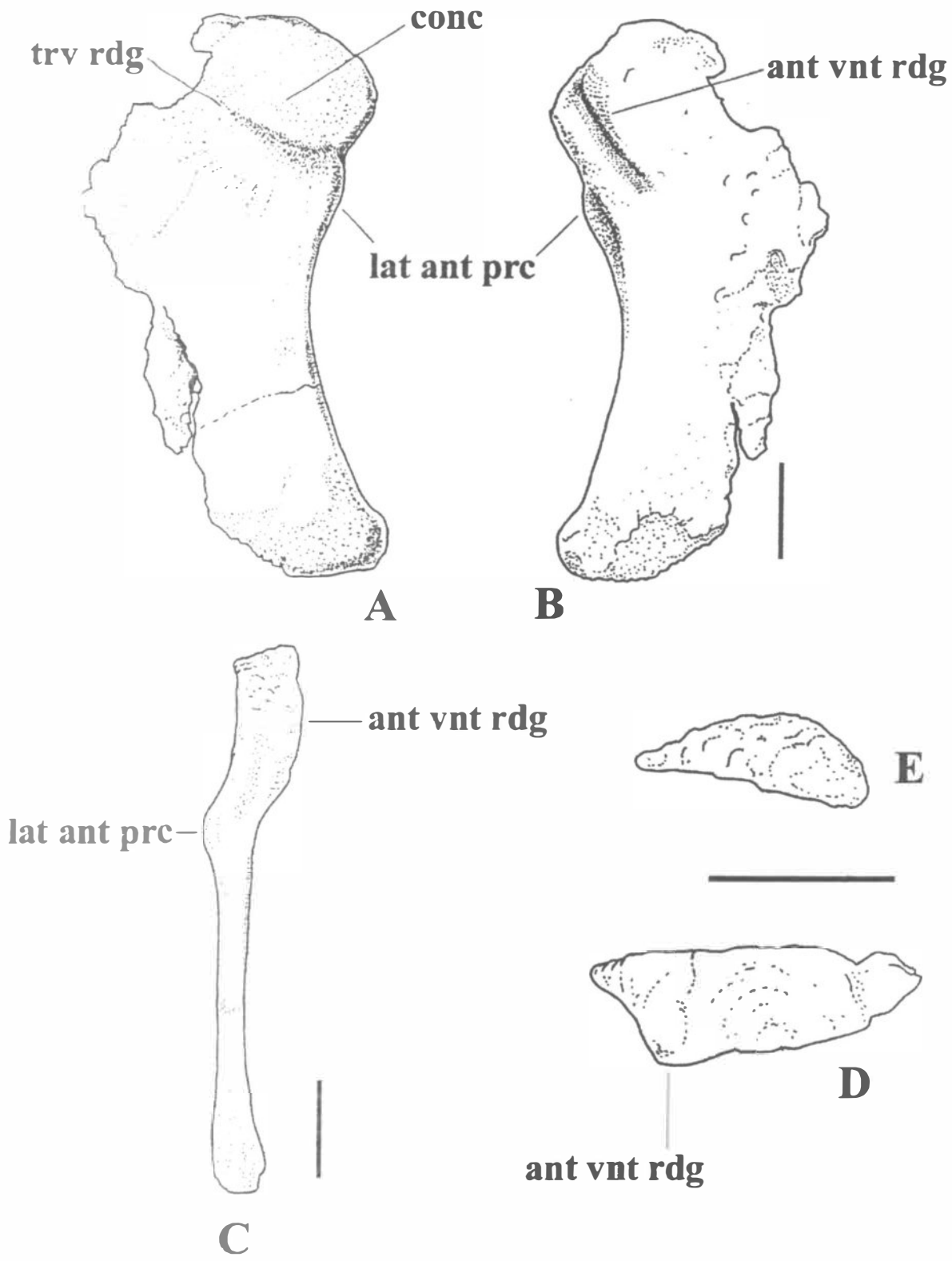


Fig. 26. Right sternal plate MCT 1589-R in A) superior (visceral), B) inferior (ventral), C) lateral, D) anterior and E) posterior views. (ant vnt rdg) antero-ventral ridge, (conc) shallow concavity, (lat ant prc) latero-anterior process, (trv rdg) transverse ridge. Scale bar equals 10 cm.

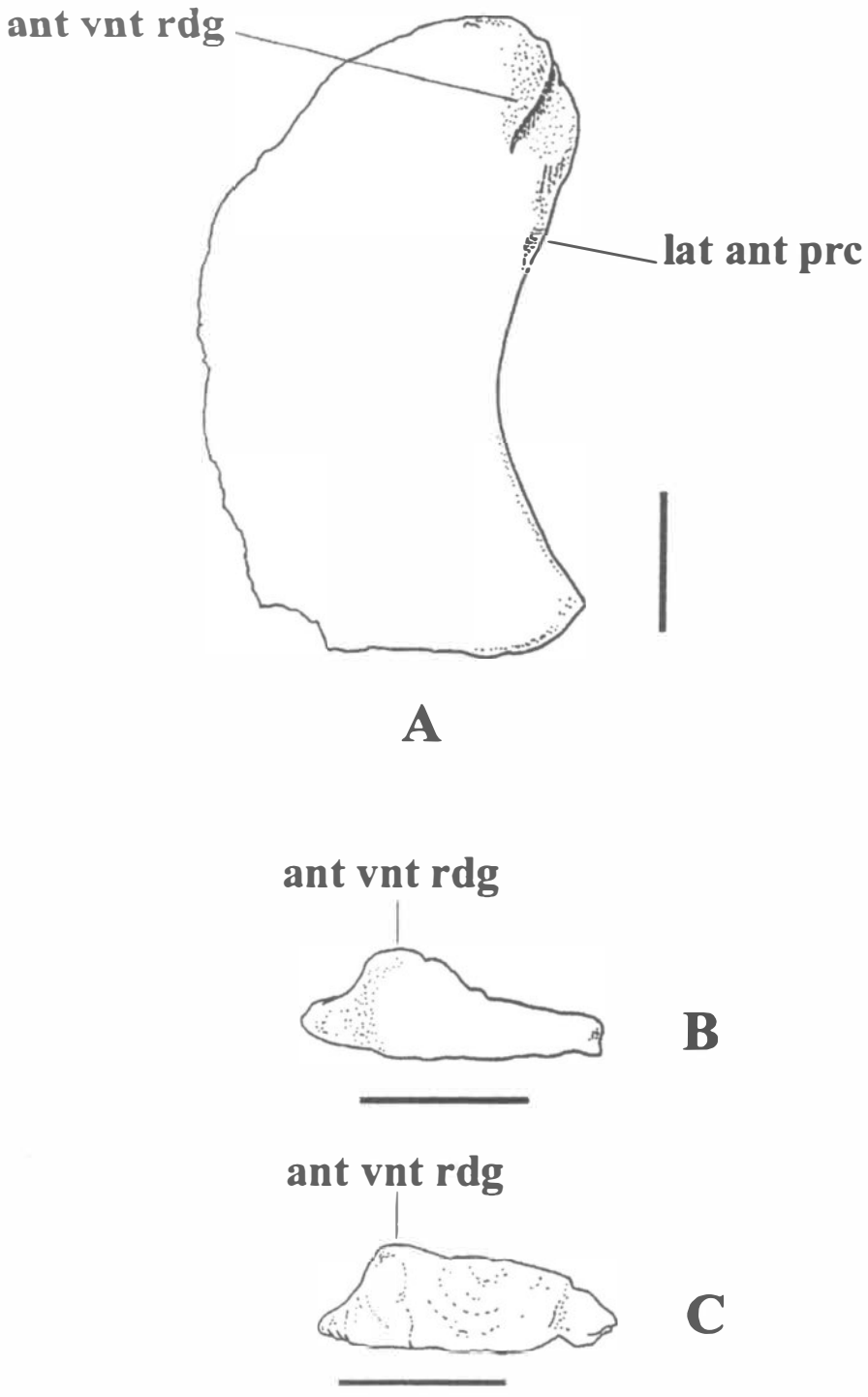


Fig. 27. Left sternal plate MCT 1690-R in A) inferior (ventral), and B) anterior views.
C) MCT 1589-R in anterior view (reversed), for comparison. (ant vnt rdg) antero-ventral ridge, (lat ant prc) latero-anterior process. Scale bar equals 10 cm.

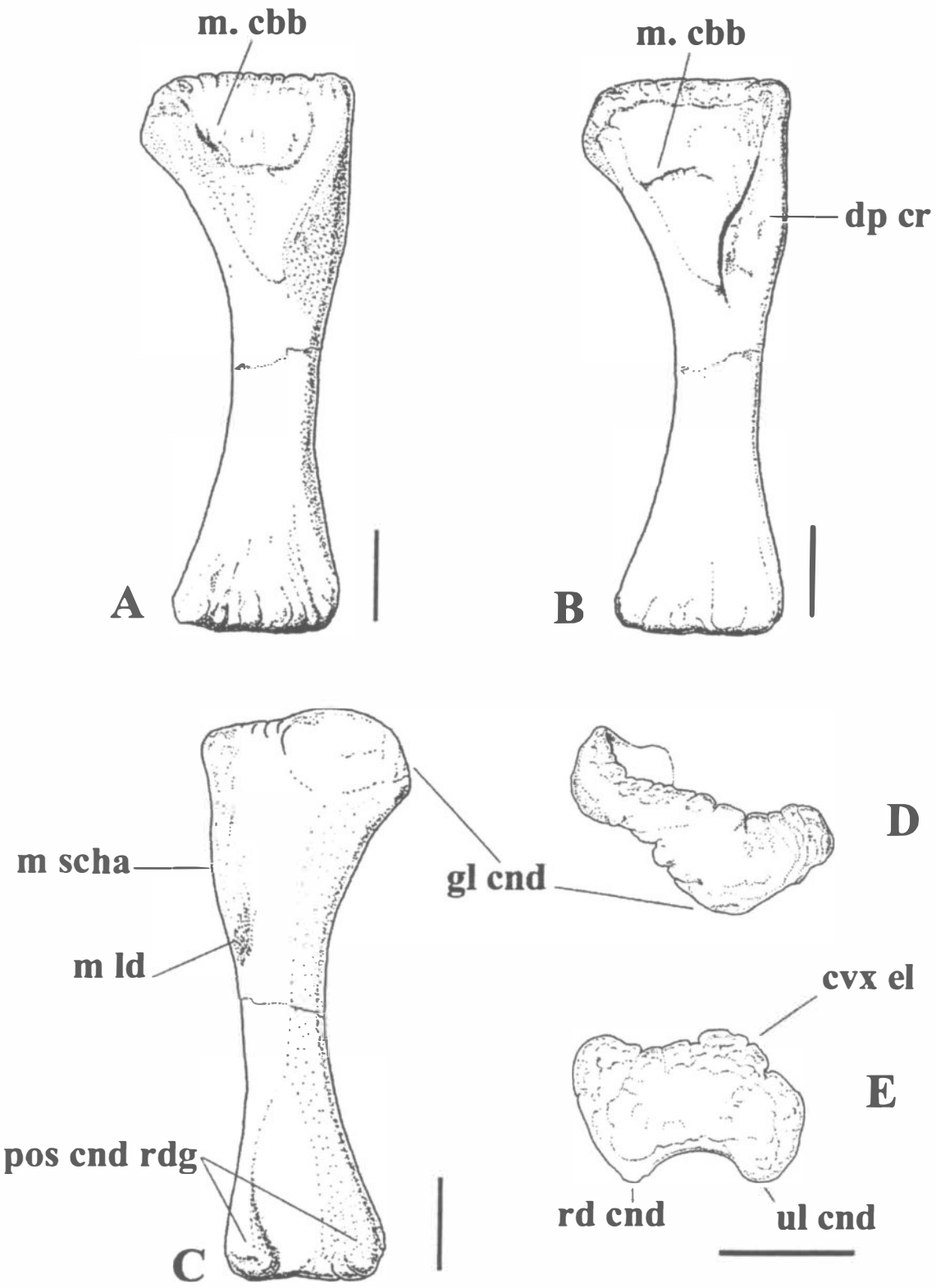


Fig 28. Left humerus MCT 1674-R in A) and B) anterior, C) posterior, D) proximal and E) distal views. (cnv el) semicircular convex elevation, (dp cr) deltopectoral crest, (gl cnd) glenoidal condyle, (lon prm) longitudinal prominence, (m. ccb) concavity for m. coracobrachialis brevis, (m. ld) insertion for m. latissimus dorsi, (m. scha) insertion for m. scapulohumeralis anterior (pos rdg) posterior supracondylar ridges, (rd cnd) radial condyle, (ul cnd) ulnar condyle. Scale bar equals 10 cm.

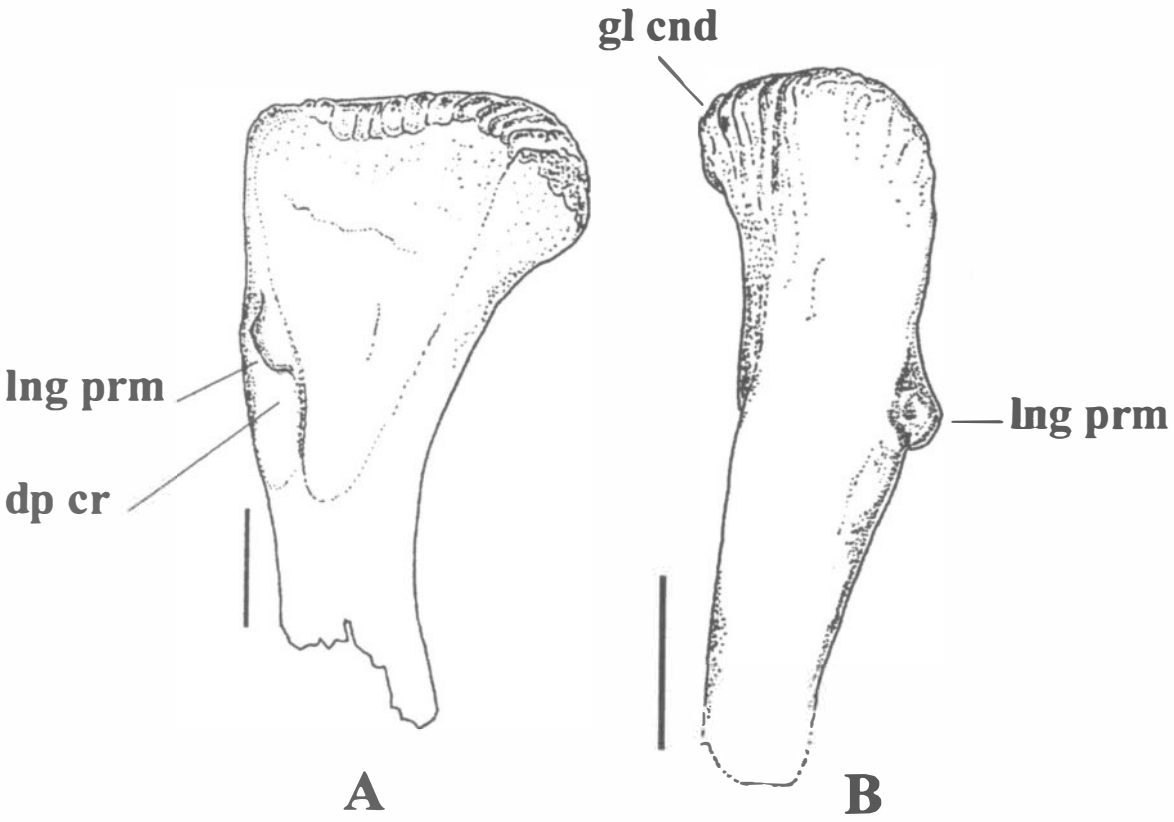


Fig. 29. Right humerus MCT 547-R in A) anterior and B) lateral views.
(dp cr) deltopectoral crest, (gl cnd) glenoidal condyle, lon prm (longitudinal prominence, (m. ccb) concavity for m. coracobrachialis brevis. Scale bar equals 10 cm.

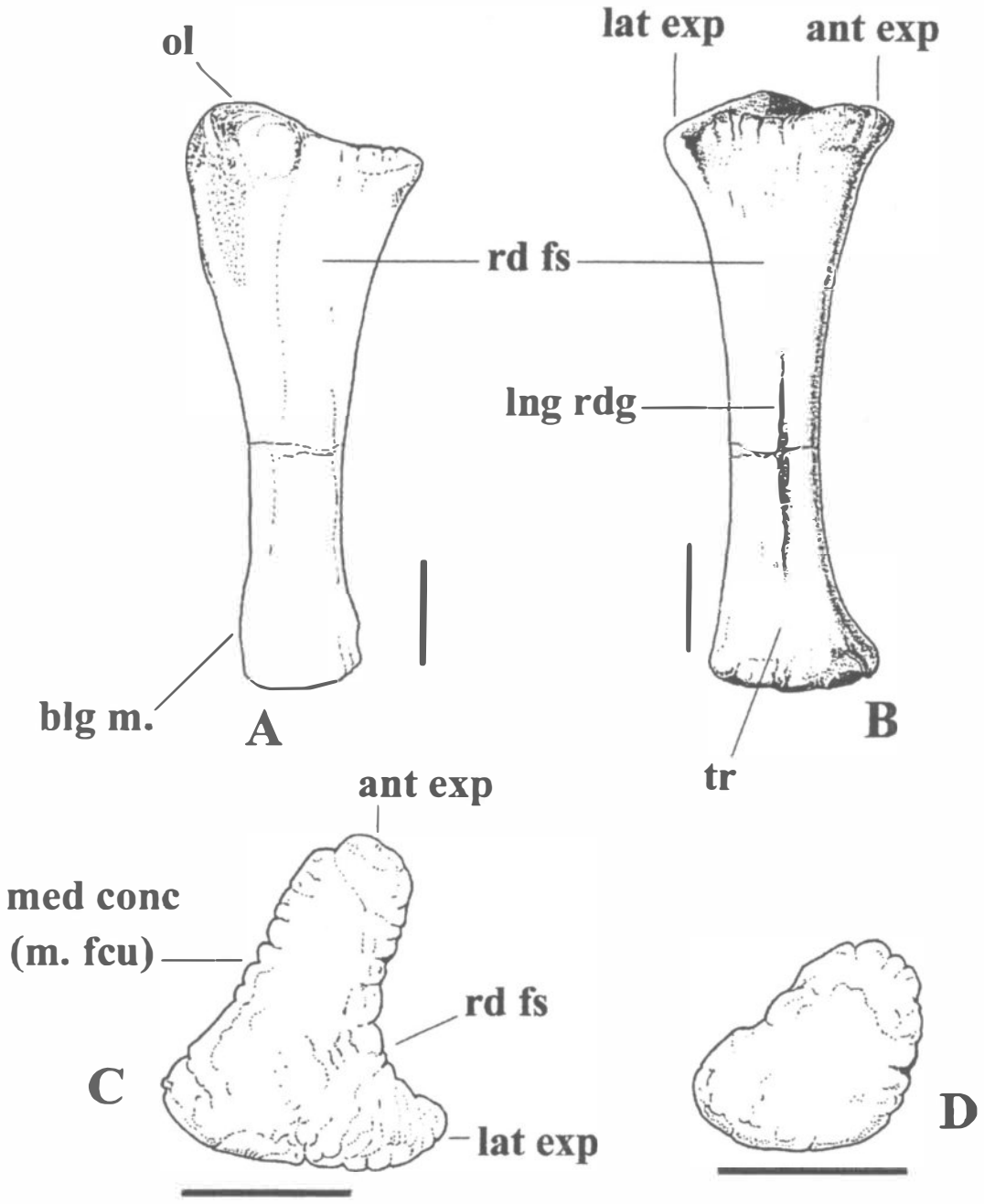


Fig. 30. Right ulna MCT 1678-R in: A) lateral, B) anterior (radial), C) proximal and D) distal views. (blg) bulge for m. extensor digitorum comunis or m. extensor carpi ulnaris, (gr exp) greater or anterior expansion (lng rdg) longitudinal ridge, (ls exp) lesser or lateral expansion (med conc) medial concavity for m. flexor carpi ulnaris, (ol) olecranon, (rd fs) radial fossa, (tr) triangular area. Scale bar equals 10 cm.

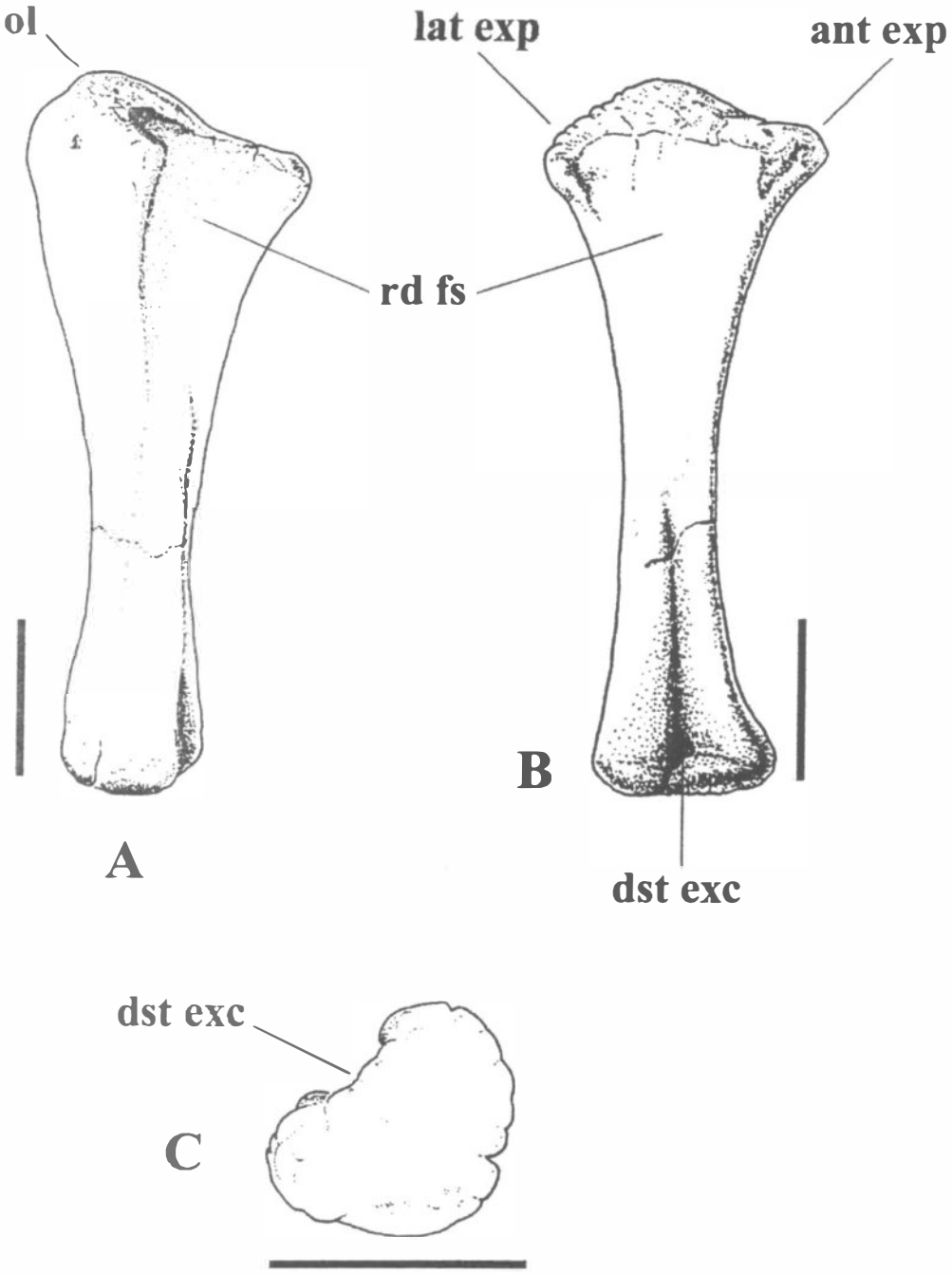


Fig. 31. Right ulna MCT 1659-R in: A) lateral, B) anterior (radial), C) distal views.
(blg) bulge for m. extensor digitorum comunis or m. extensor carpi ulnaris, (dst exc) distal excavation, (gr exp) greater or anterior expansion (lng rdg) longitudinal ridge, (ls exp) lesser or lateral expansion (med conc) medial concavity for m. extensor carpi ulnaris, (ol) olecranon, (rd fs) radial fossa. Scale bar equals 10 cm.

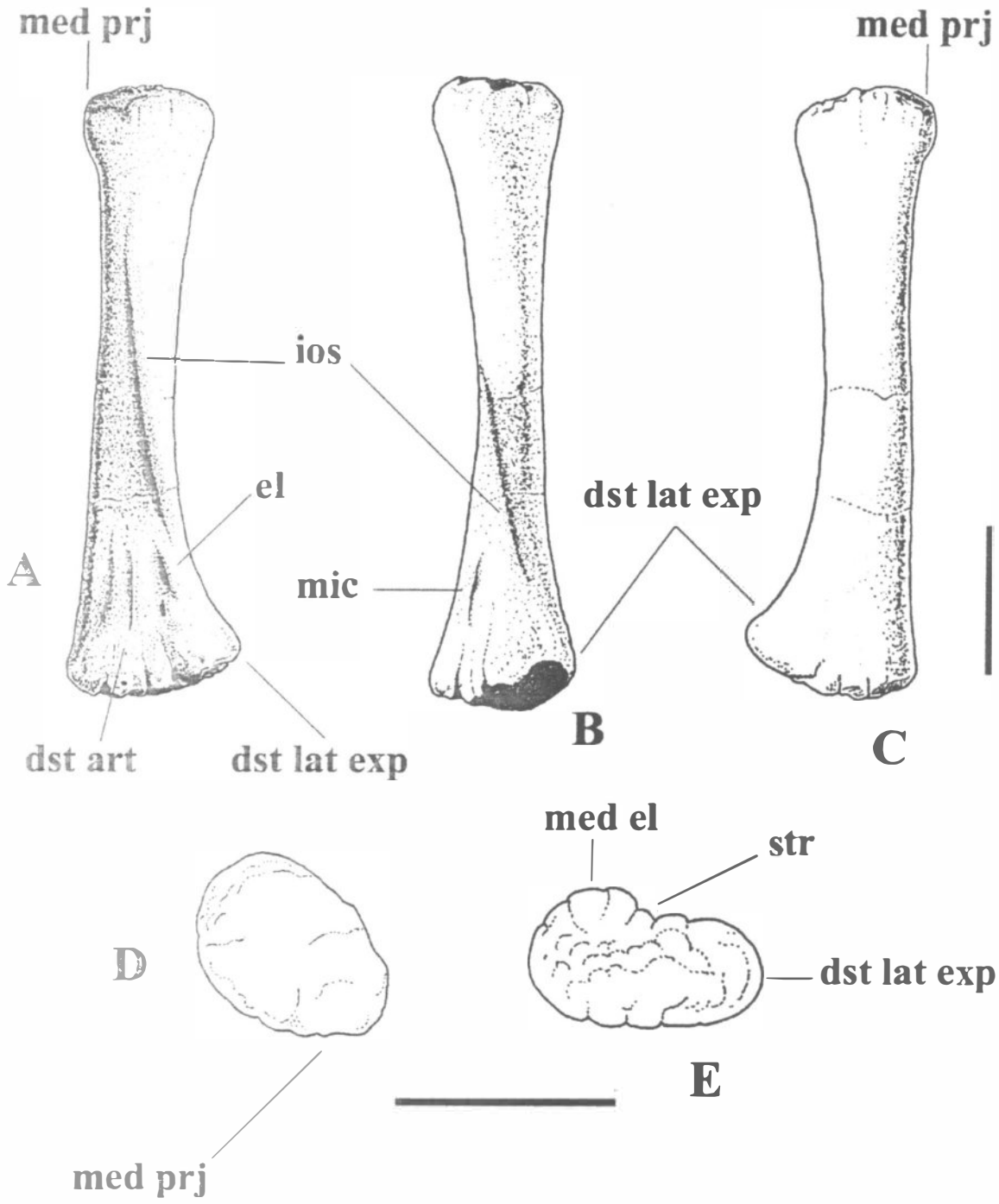


Fig. 32. Right radius MCT 1637-R in: A) posterior (ulnar), B) lateral, C) anterior, D) proximal and E) distal views. (dst art) distal articular area, (dst lat exp) distal lateral expansion, (el) small elevation at end of interosseus ridge. (ios) interosseus ridge. (med el) medial elevation, (med prj) medial projection, (mic) micro-ridge. (str) subtriangular depression. Scale bar equals 10 cm.

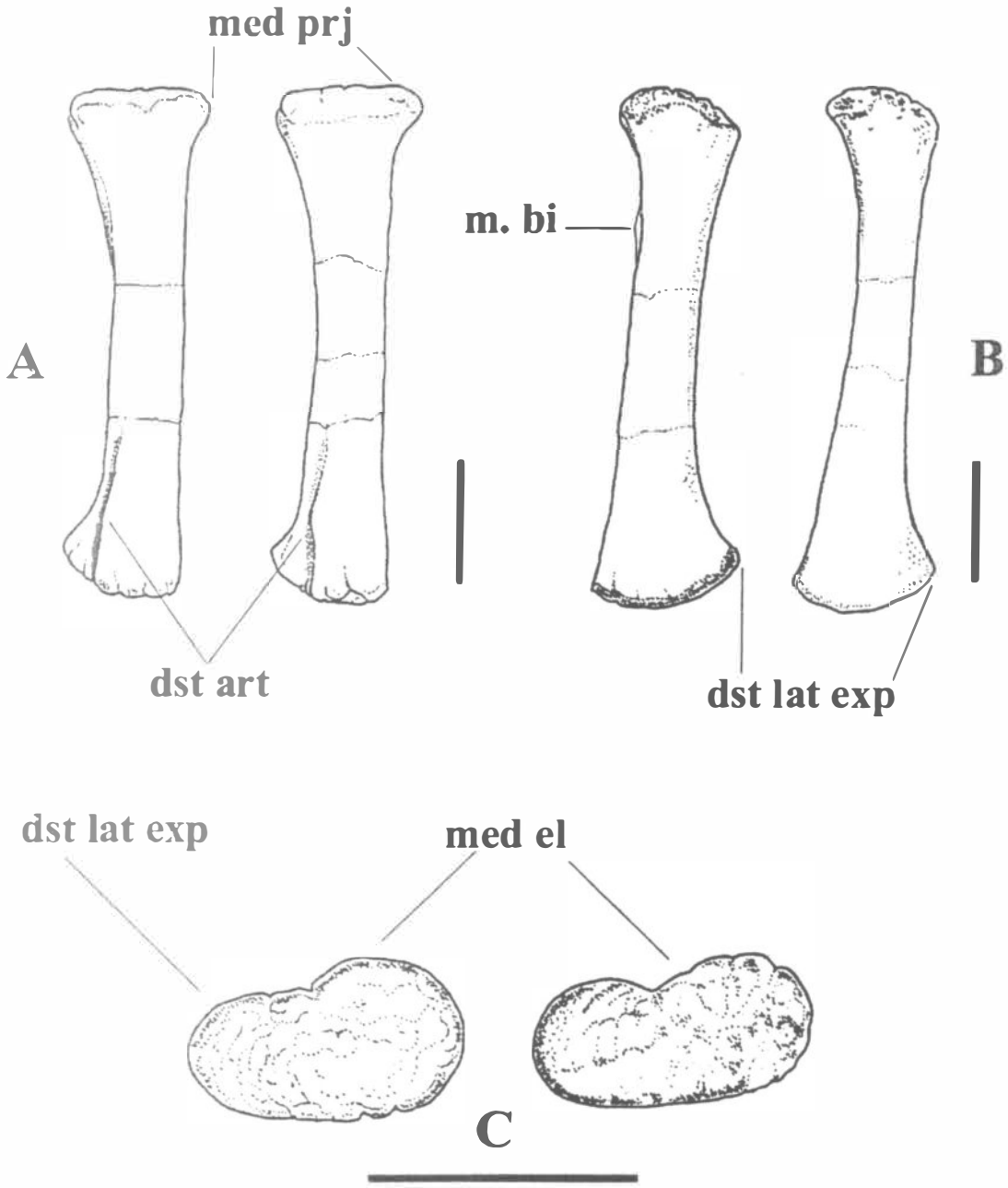


Fig. 33. Left radii MCT 1638-R and MCT 1649-R in A) medio-posterior, B) anterior and C) distal views, for comparison between morphotypes 1 and 2. (MCT 1638 at left side).
(dst art) distal articular area, (dst lat exp) distal lateral expansion, (m. bi) insertion for muscle biceps/brachialis inferior, (med el) medial elevation, (med prj) medial projection. Scale bar equals 10 cm.

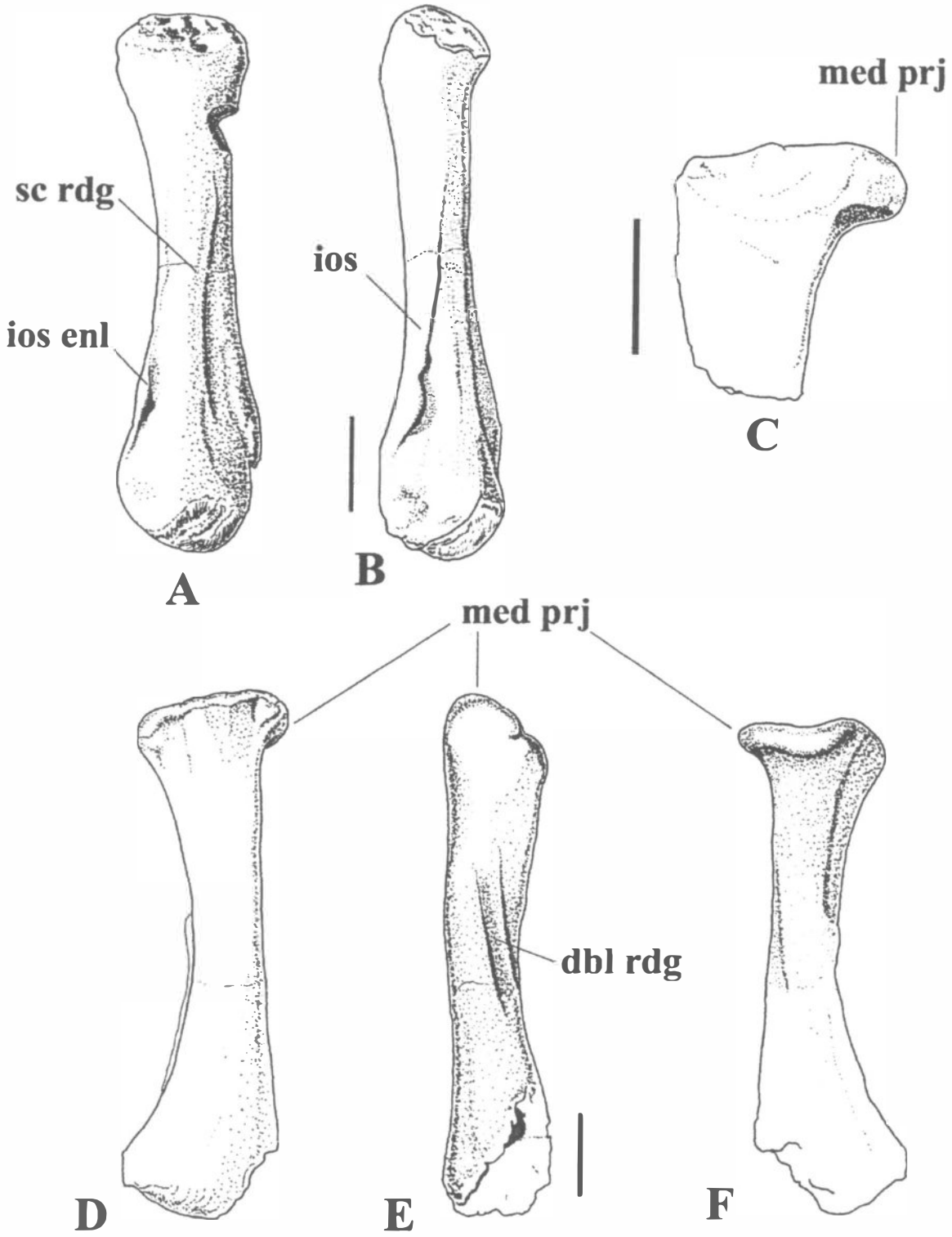


Fig. 34. Radii of morphotypes 3 and 4:
Right radius MCT 1595-R in: A) posterior (ulnar) and B) medial views
C) Radius MCT 1673-R (just head), to show extreme development of medial projection.
Right radus MCT 1707-R in D) anterior, E) medial, and F) posterior views.
(dbl rdg) double ridge, (ios enl) enlargement of interosseus, (med prj) medial projection (sc rdg) second ridge. Scale bar equals 10 cm.

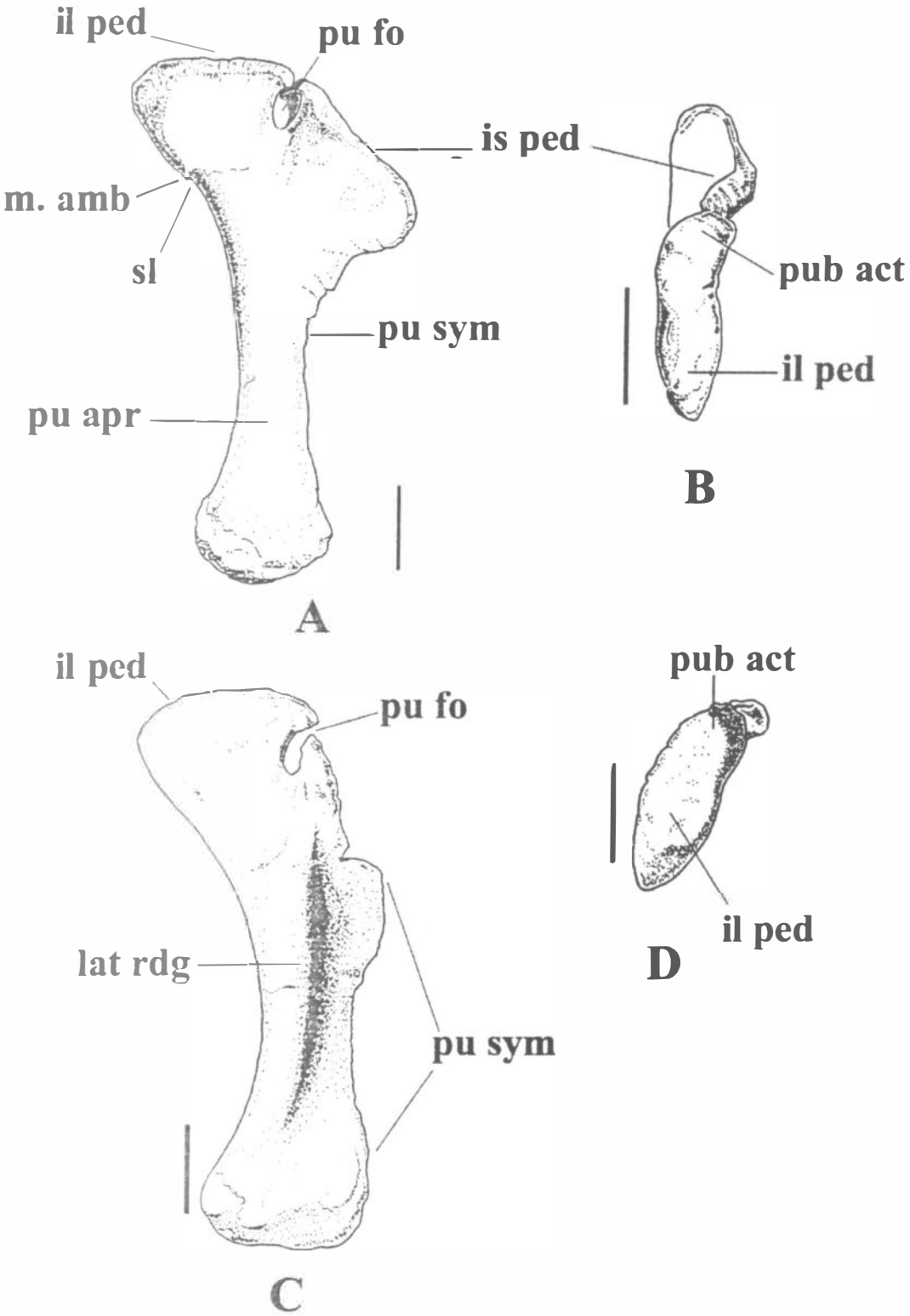


Fig. 35. Left pubis MCT 1592-R in A) lateral and B) proximal views
Left pubis MCT 1641-R in C) lateral and D) proximal views
(acet) acetabular portion of pubis, (il ped) iliac pedicle, (is ped) ischial pedicle, (lat rdg) lateral ridge, (m. amb) insertion of m. ambiens, (pu ap) pubic apron, (pu fo) pubic foramen, (pu sym) pubic symphysis, (sl) slope. Scale bar equals 10 cm.

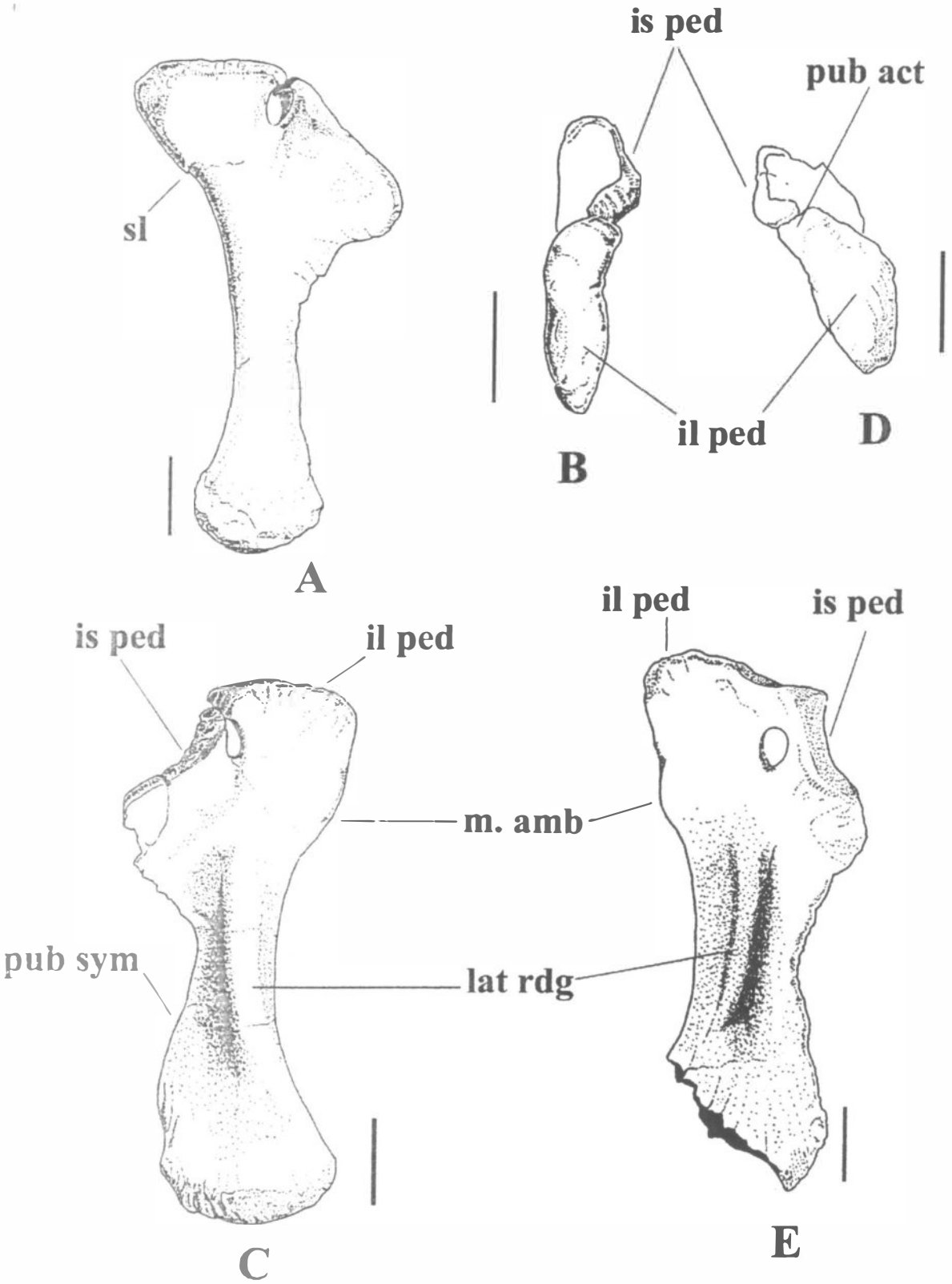


Fig. 36. Left pubis MCT 1592-R in A) lateral and B) proximal views
Right pubis MCT 1640-R in C) lateral and D) proximal views
E) Left pubis MCT 1677-R in lateral view.
(acet) acetabular portion of pubis, (il ped) iliac pedicle, (is ped) ischial pedicle, (lat rdg) lateral ridge, (m. amb) insertion of m. ambiens, (pu ap) pubic apron, (pu fo) pubic foramen, (pu sym) pubic symphysis, (sl) slope. Scale bar equals 10 cm.

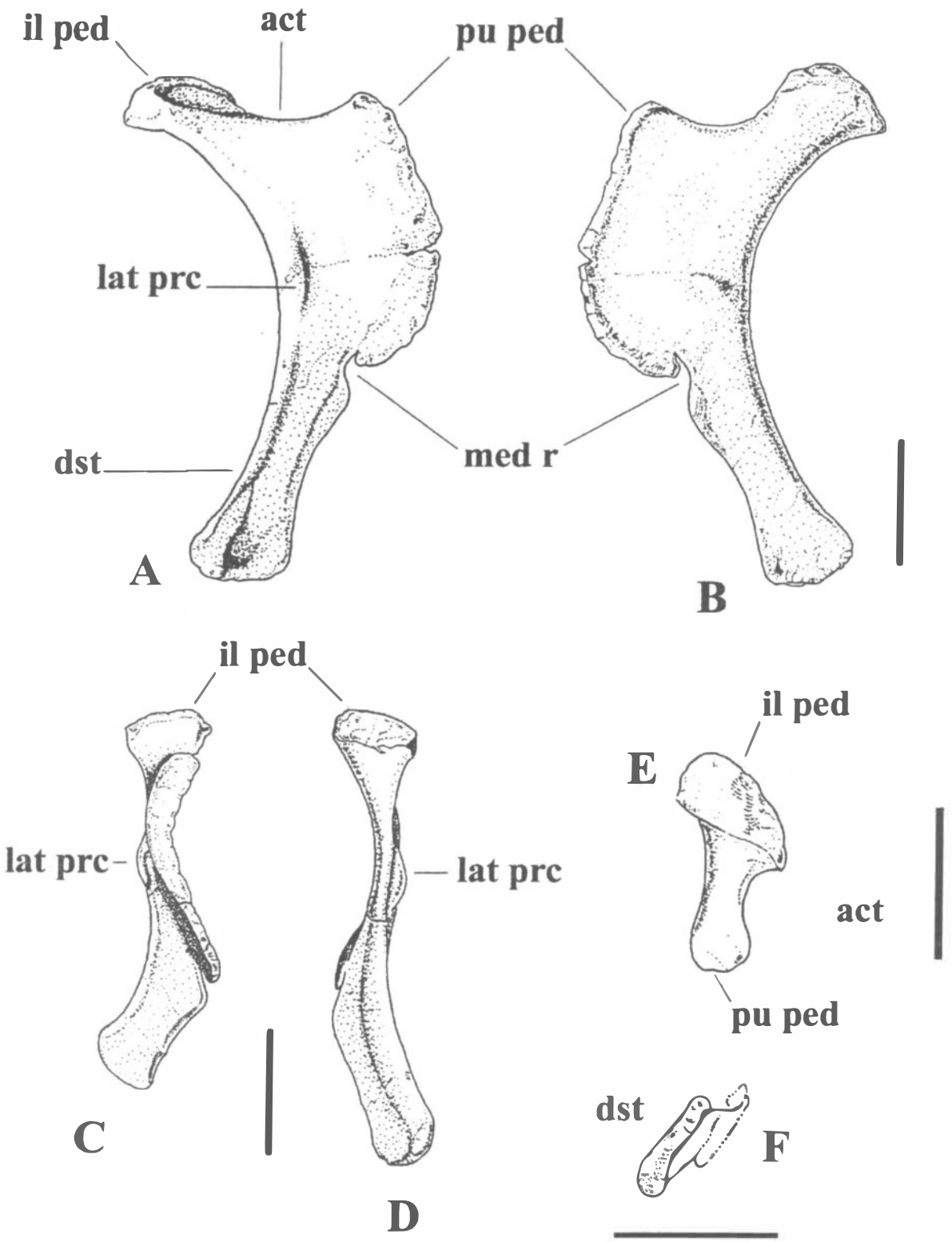


Fig. 37. Right ischium MCT 1586 in A) inferior, B) superior, C) anterior, D) posterior, E) proximal and F) distal views.
(dst) distal shaft, (il ped) iliac pedicle, (is sym) ischial symphysis, (lat prc) lateral process, (med r) medial reentrance, (pu ped) pubic pedicle. Scale bar equals 10 cm.

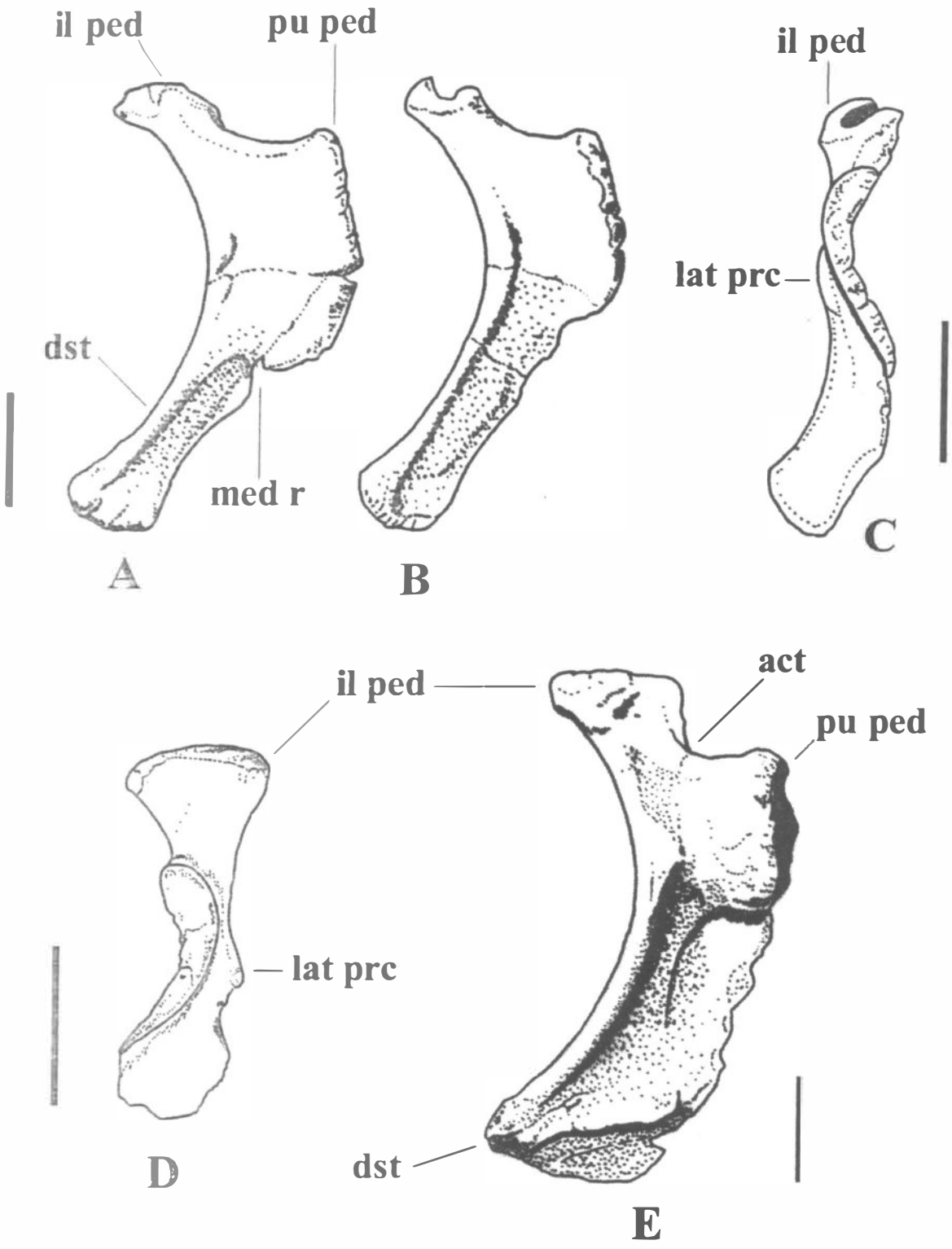


Fig. 38. Ischia from Peirópolis
A) Right ischium MCT 1586-R A) inferior view
Right ischium MCT 1655-R in B) inferior and C) anterior views.
D) Left ischium MCT 1654-R in anterior view
E) Left ischium MCT 1689-R in inferior view
(dst) distal shaft, (il ped) iliac pedicle, (is sym) ischial symphysis, (lat prc) lateral process, (med r) medial reentrance, (pu ped) pubic pedicle. Scale bar equals 10 cm.

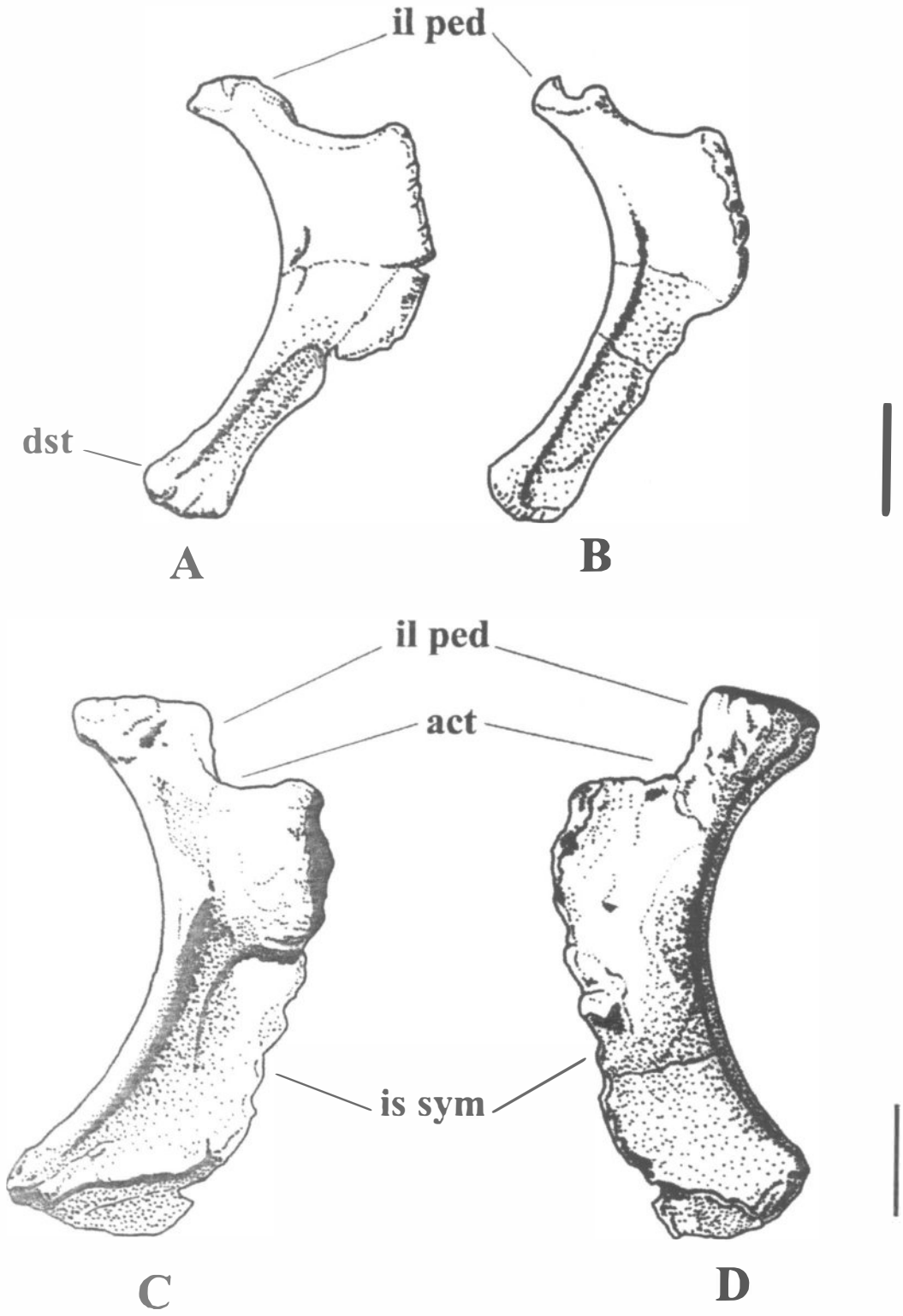


Fig. 39. Ischia from Peirópolis
A) Right ischium MCT 1586-R in inferior view
B) Right ischium MCT 1655-R in inferior view
Left ischium MCT 1689-R in C) inferior and D) superior views
(dst) distal shaft. (il ped) iliac pedicle. (is sym) ischial symphysis, (lat prc) lateral process, (med r) medial reentrance. (pu ped) pubic pedicle. Scale bar equals 10 cm.

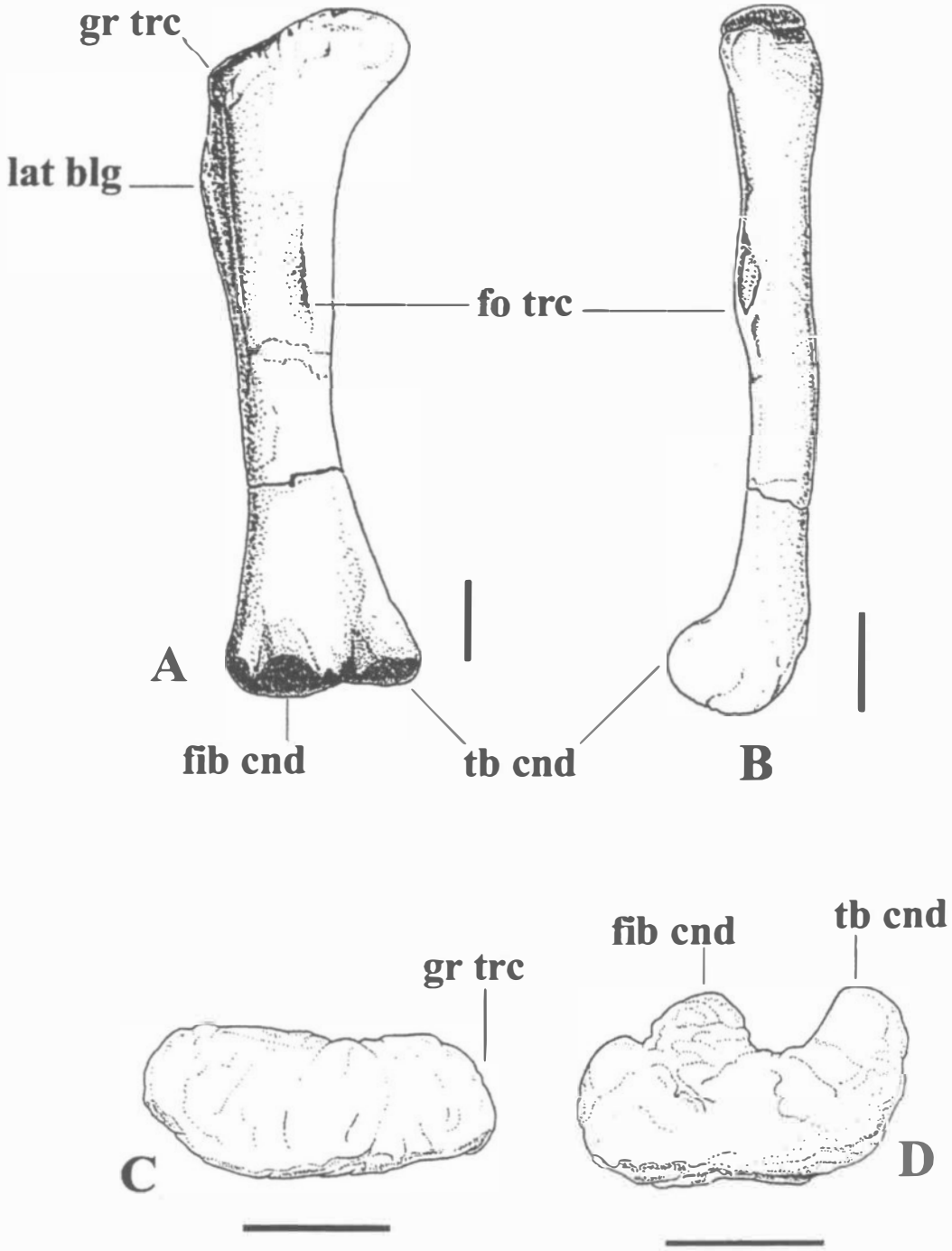


Fig. 40. Left femur MCT 1601-R in: A) posterior, B) medial, C) proximal and D) distal views. (fib cnd) fibular condyle, (ft) fourth trochanter, (gr trc) greater trochanter, (lat blg) lateral bulge, (tb cnd) tibial condyle. Scale bar equals 10 cm.

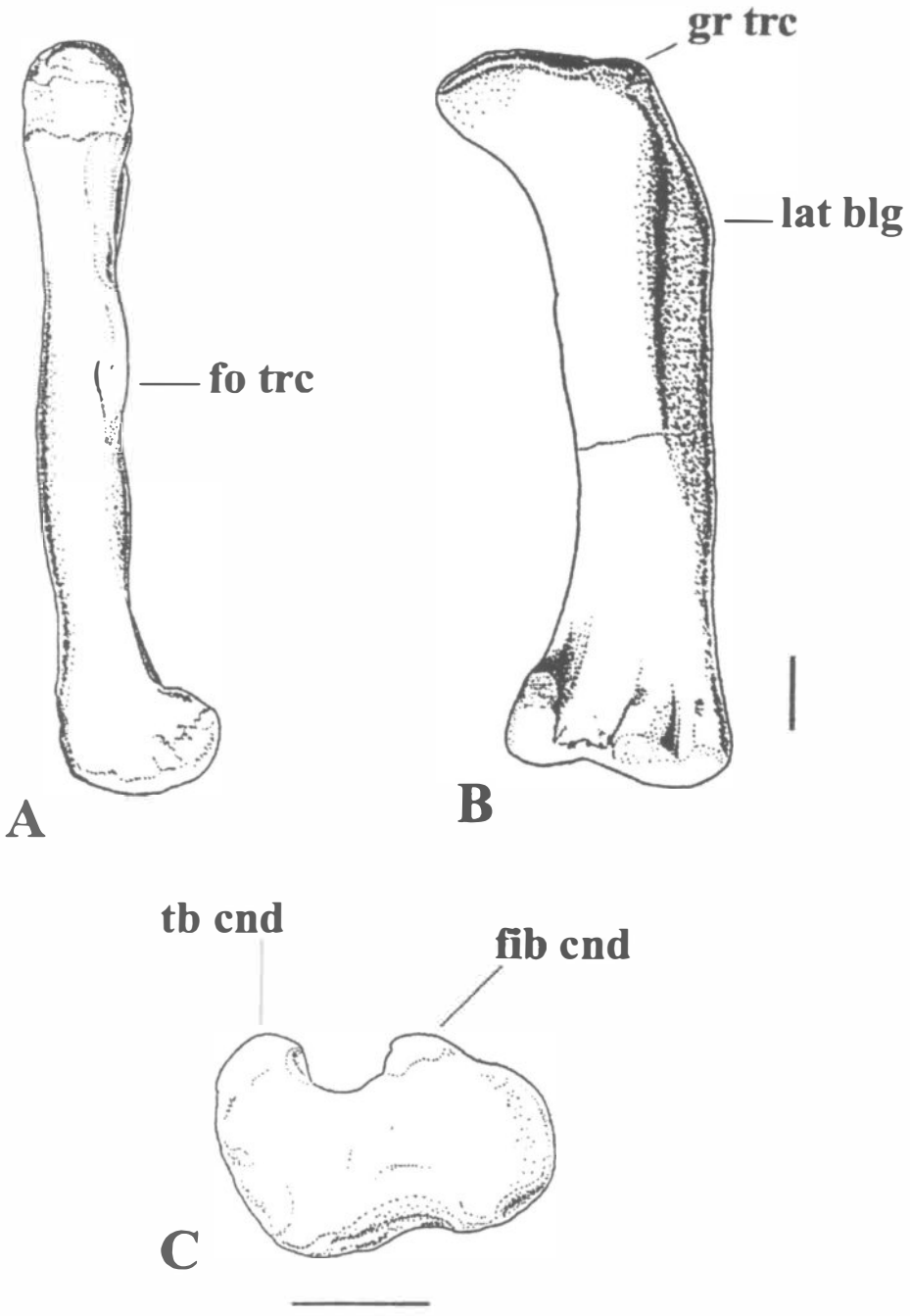


Fig. 41. Right femur MCT 1692-R in: A) medial, B) posterior and C) distal views.
(fib cnd) fibular condyle, (ft) fourth trochanter, (gr trc) greater trochanter, (lat blg) lateral bulge, (tb cnd) tibial condyle. Scale bar equals 10 cm.

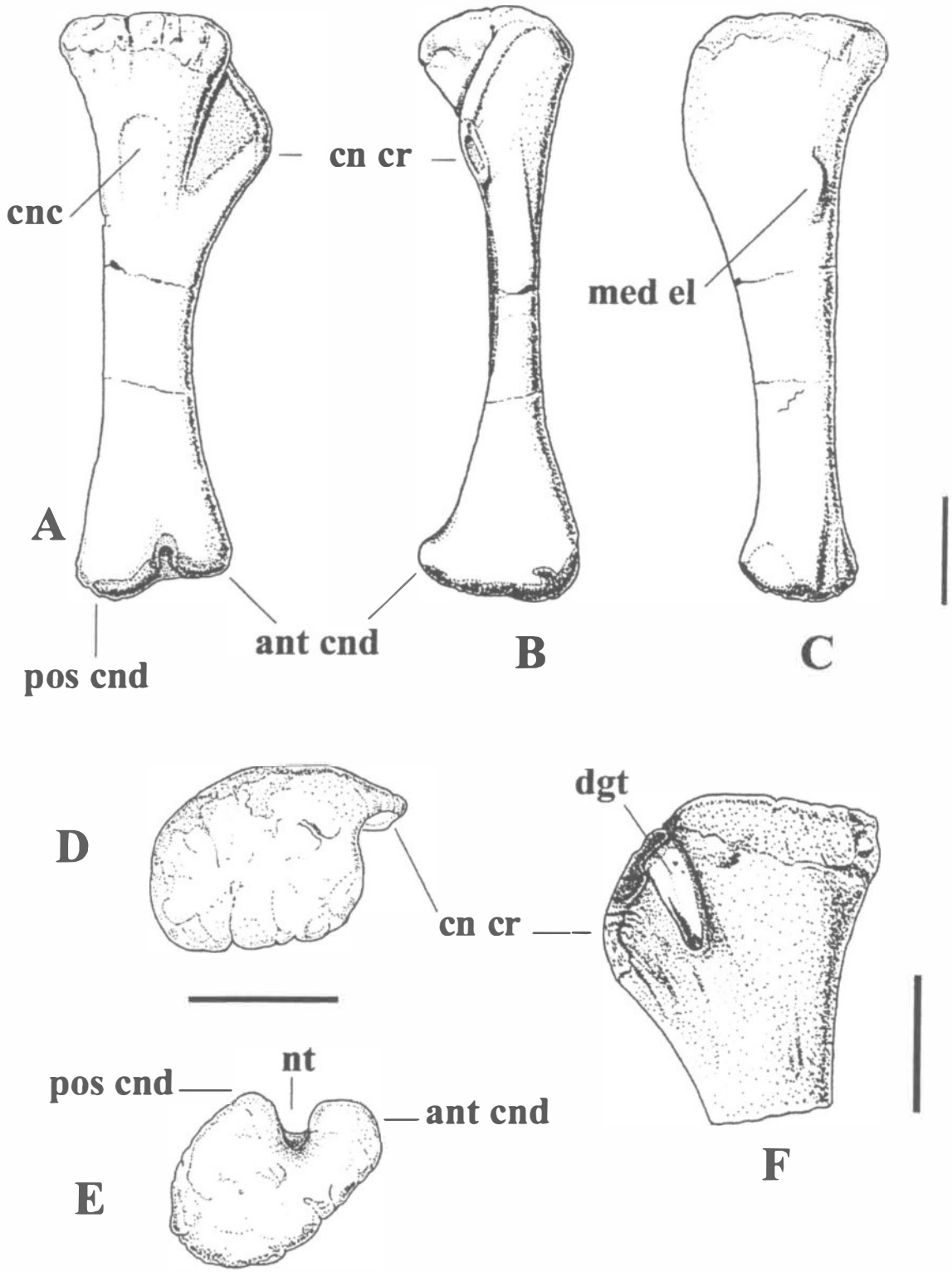


Fig. 42. Right tibia MCT 1681-R in A) lateral, B) anterior, C) medial, D) proximal and E) distal views. F) Left tibia MCT 1587-R (just head).
(ant cnd) anterior condyle, (cn cr) cnemial crest, (conc) concavity on head of tibia, (med el) emdial elevation, (not) notch, (pos cnd) posterior condyle. Scale bar equals 10 cm.

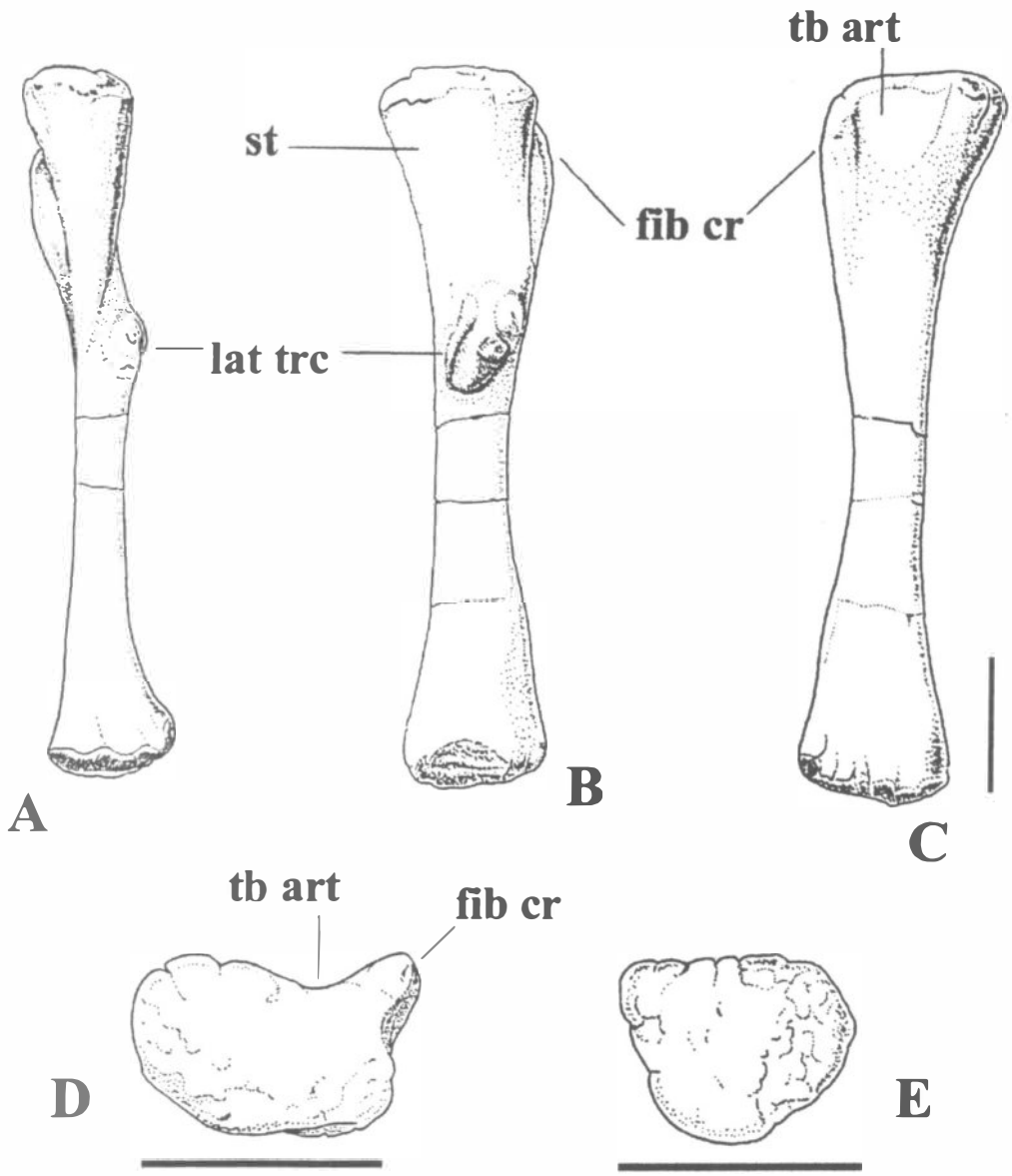


Fig. 43. Right fibula MCT 1660-R in: A) posterior, B) lateral, C) medial, D) proximal and E) distal views. (fib cr) fibular crest, (lat trc) lateral trochanter/tuberosity, (st) stalk, (tb art) tibial articular surface. Scale bar equals 10 cm.

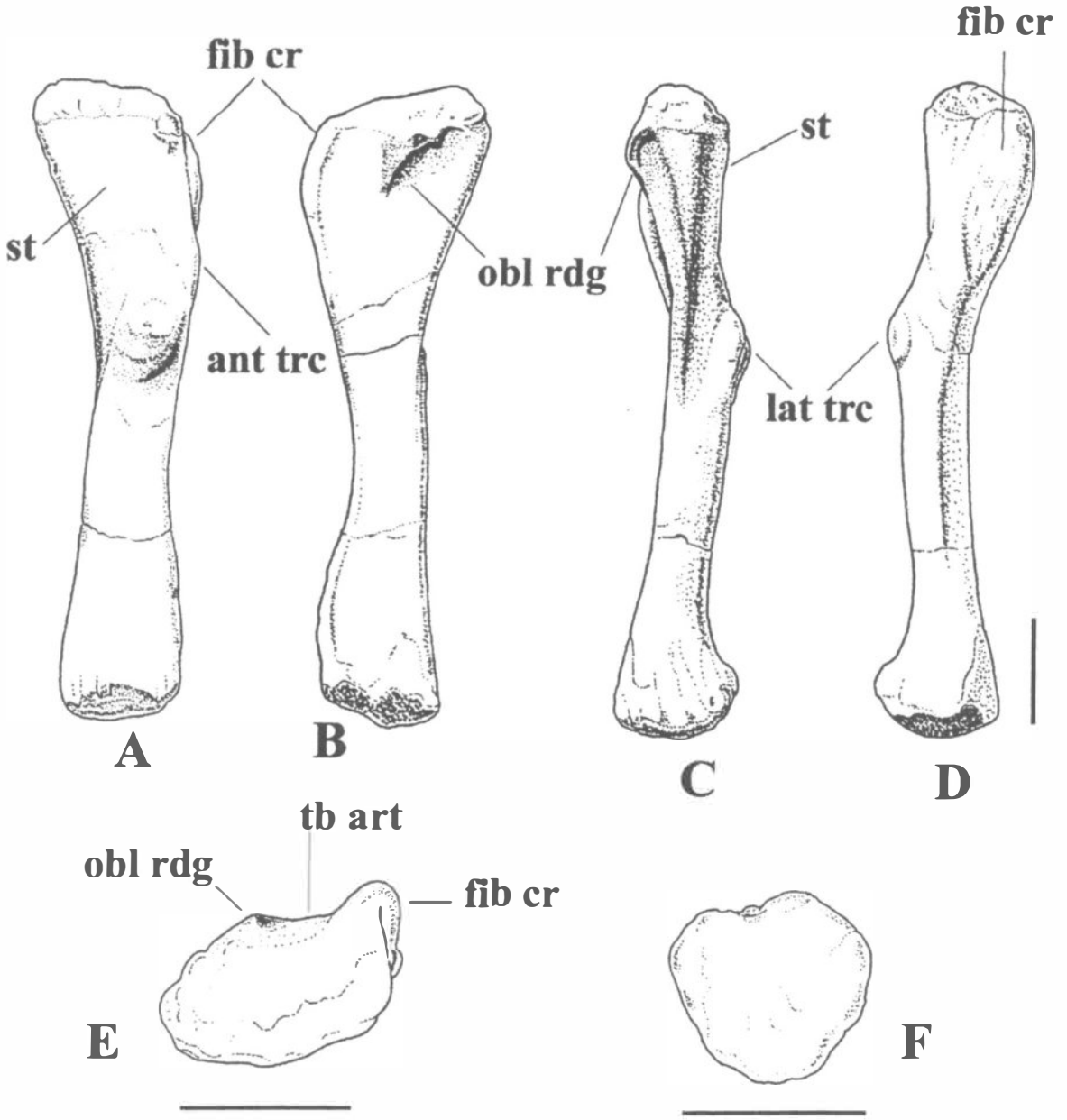


Fig. 44. Right fibula MCT 1608-R in: A) lateral, B) medial, C) posterior, D) anterior, E) proximal and F) distal views. (ant trc) anterior trochanter, (fib cr) fibular crest, (lat trc) lateral trochanter/tuberosity, (obl rdg) oblique ridge, (st) stalk, (tb art) tibial articular surface. Scale bar equals 10 cm.

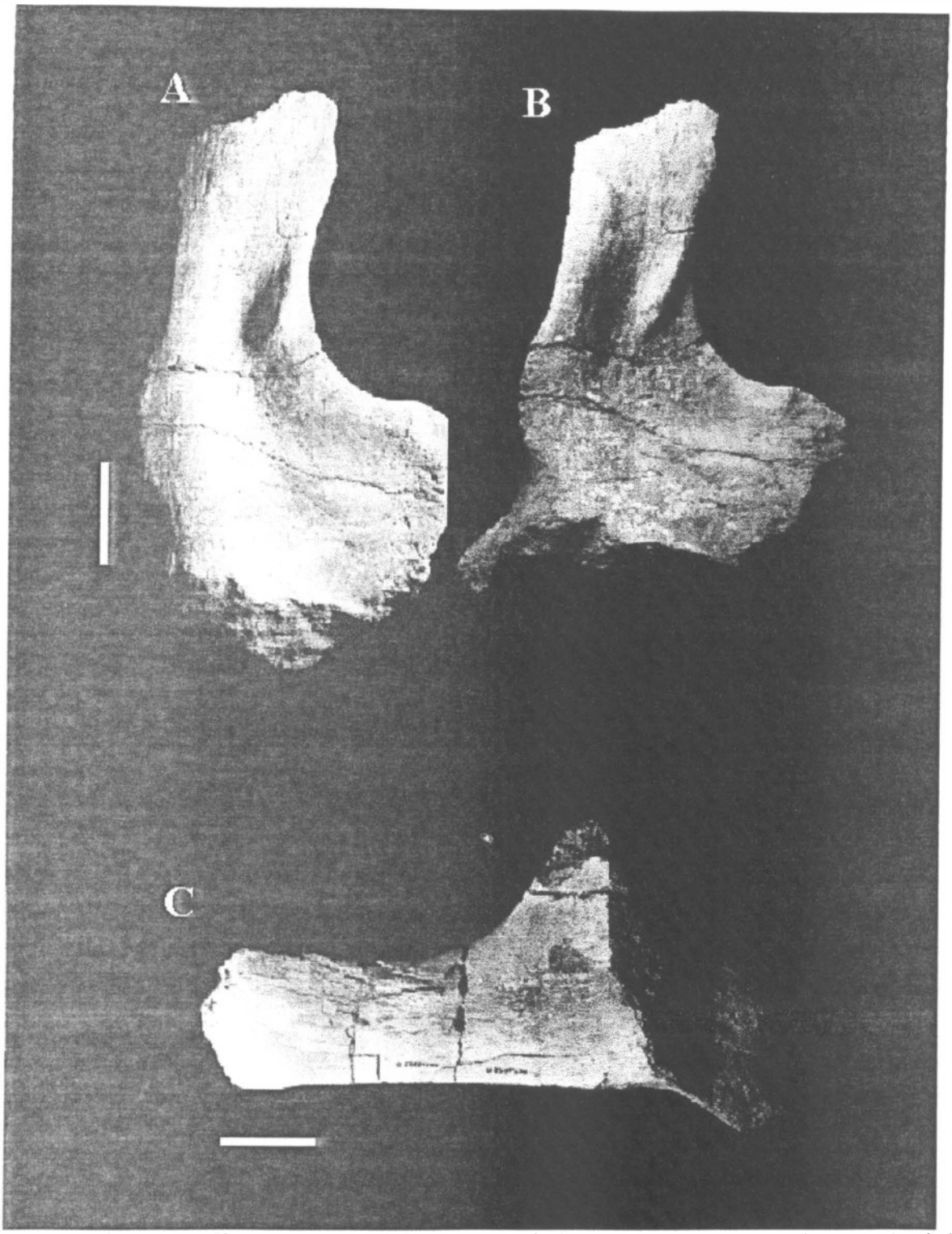


Fig. 45. Left scapula MCT 1599-R in medial view: A) with light comming from the right; B) with light comming from the left, to highlight medial prominence.
C) Left scapula MCT 1642-R in medial view. Scale bar = 10 cm.

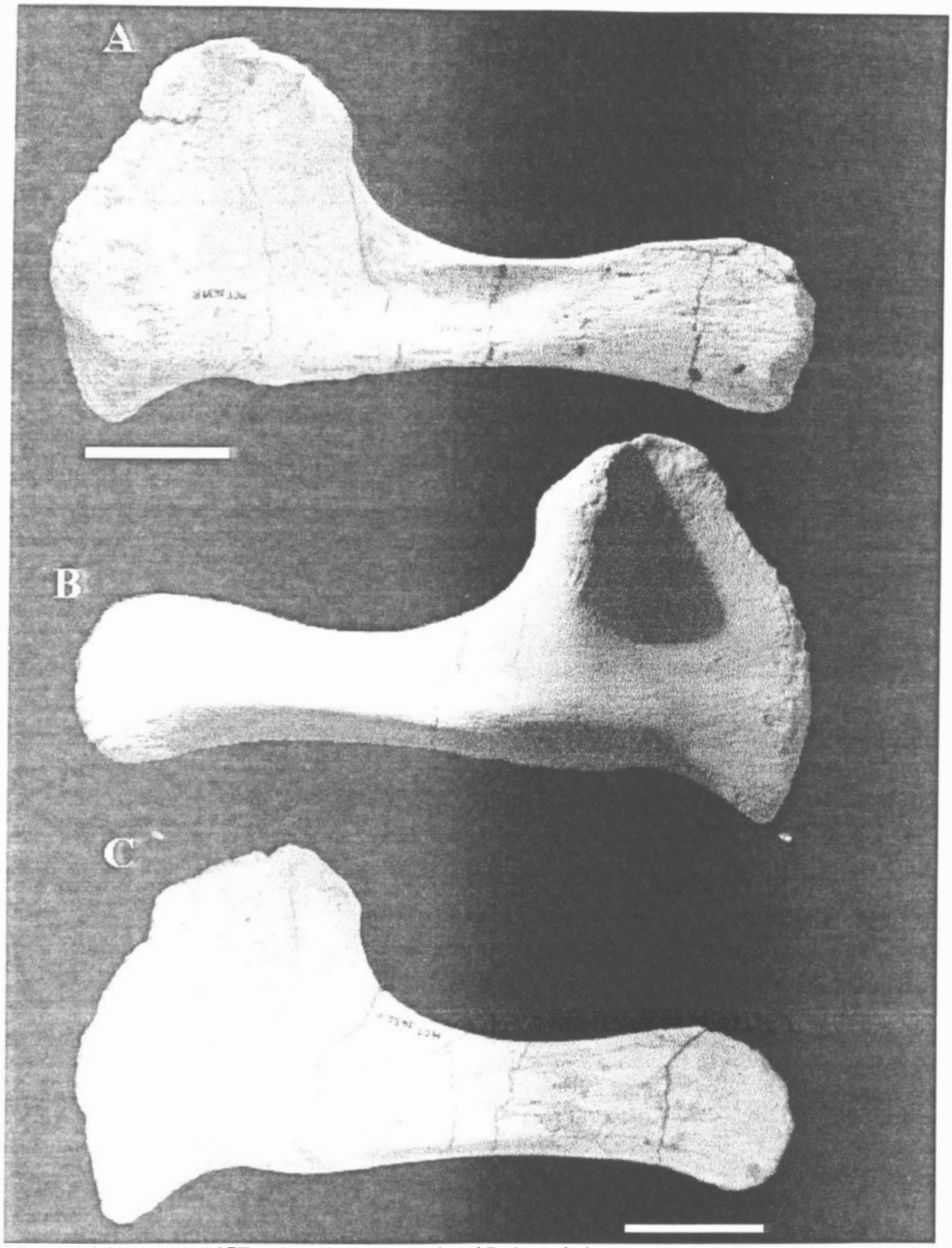


Fig. 46. Right scapula MCT 1639-R in: A) medial and B) lateral view.
C) Left scapula MCT 1652 in lateral view. Scale bar = 10 cm.

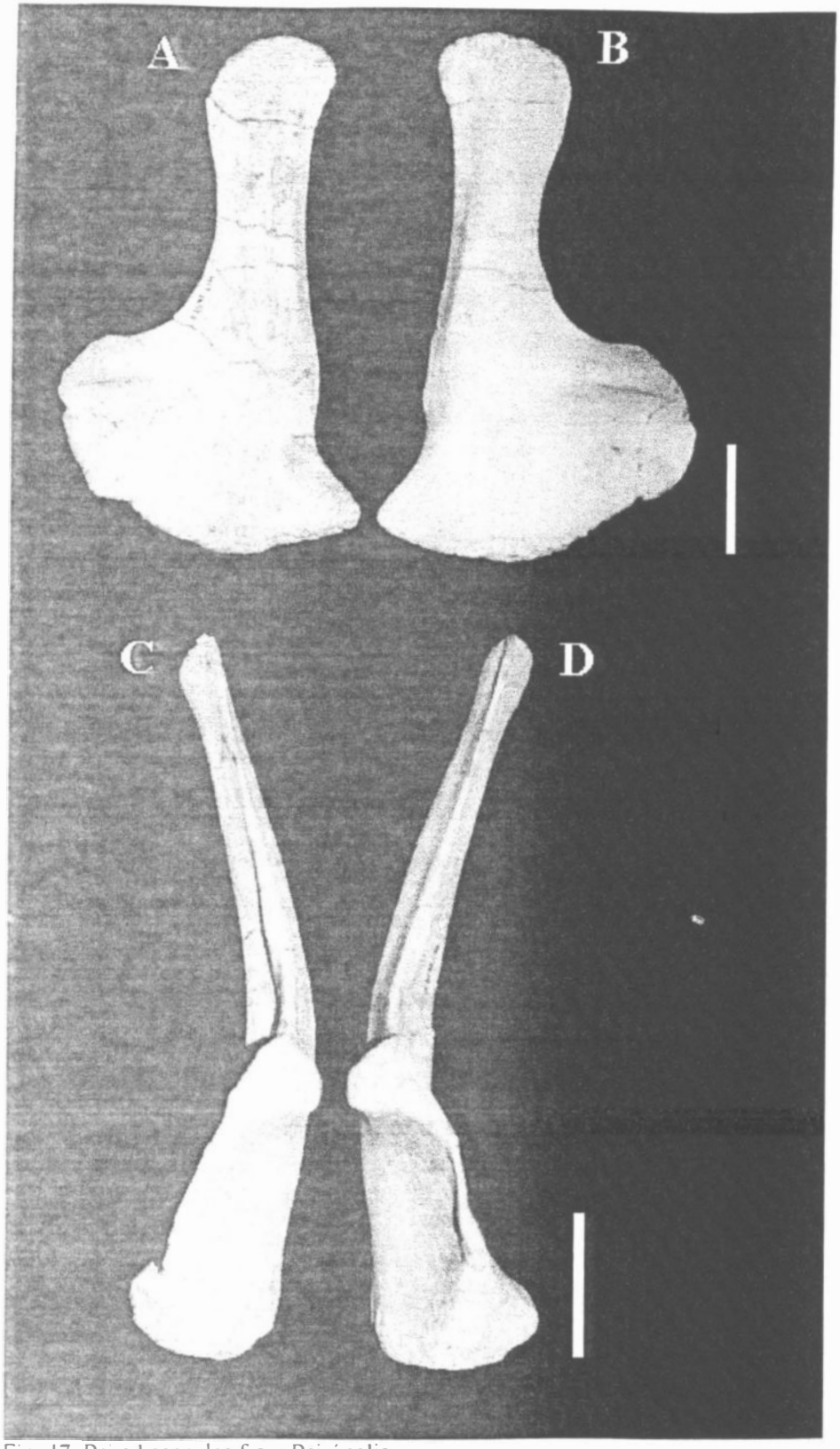


Fig. 47. Paired scapulae from Peirópolis.
MCT 1652-R in A) lateral and C) superior views.
MCT 1639-R in B) lateral and D) superior views.
A and B; C and D to the same scale. Scale bar = 10 cm.

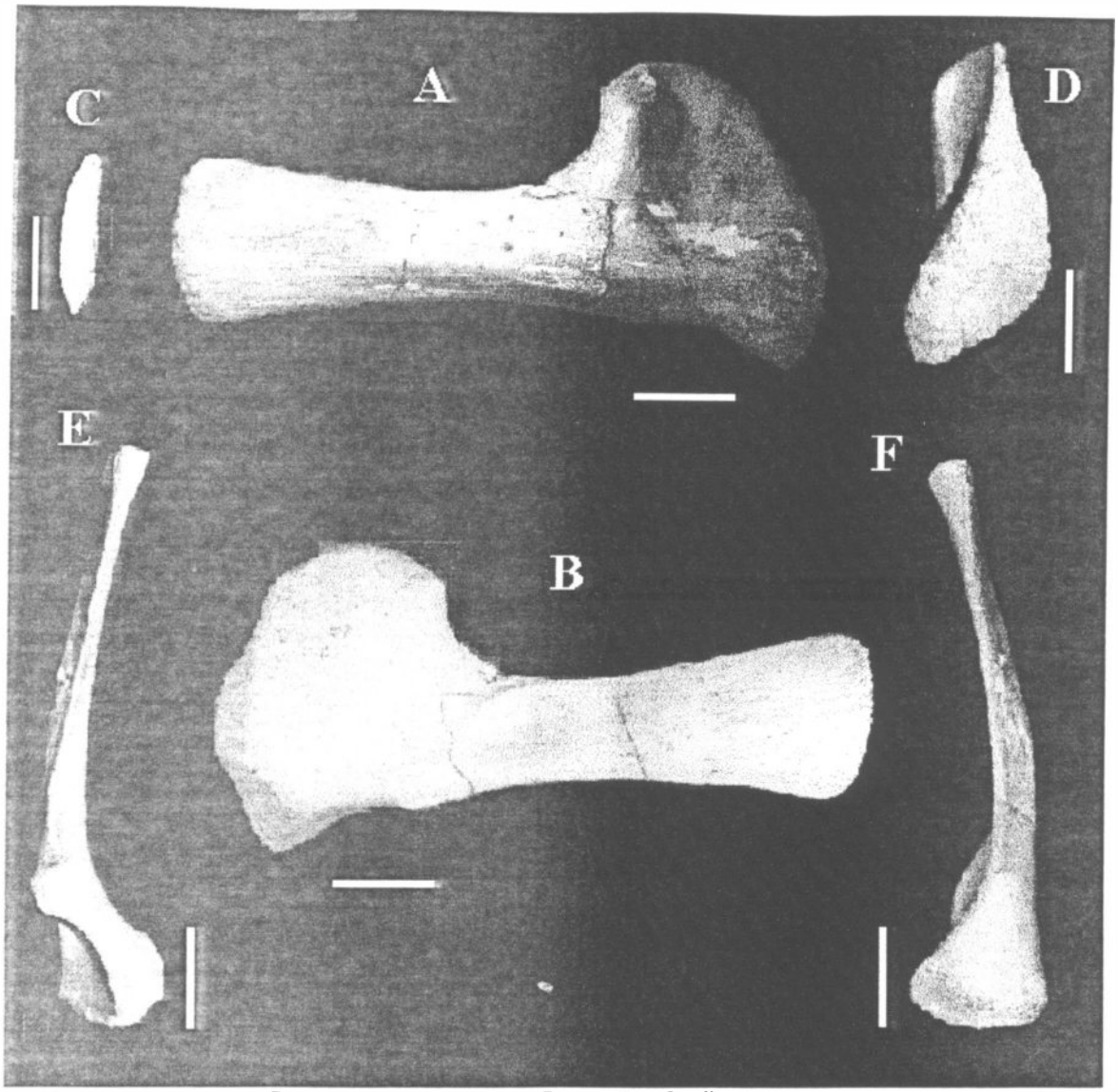


Fig. 48. Right scapula MCT 1680-R in: A) lateral; B) medial; C) distal; D) anterior; E) superior, F) inferior views. Scale bar = 10 cm.

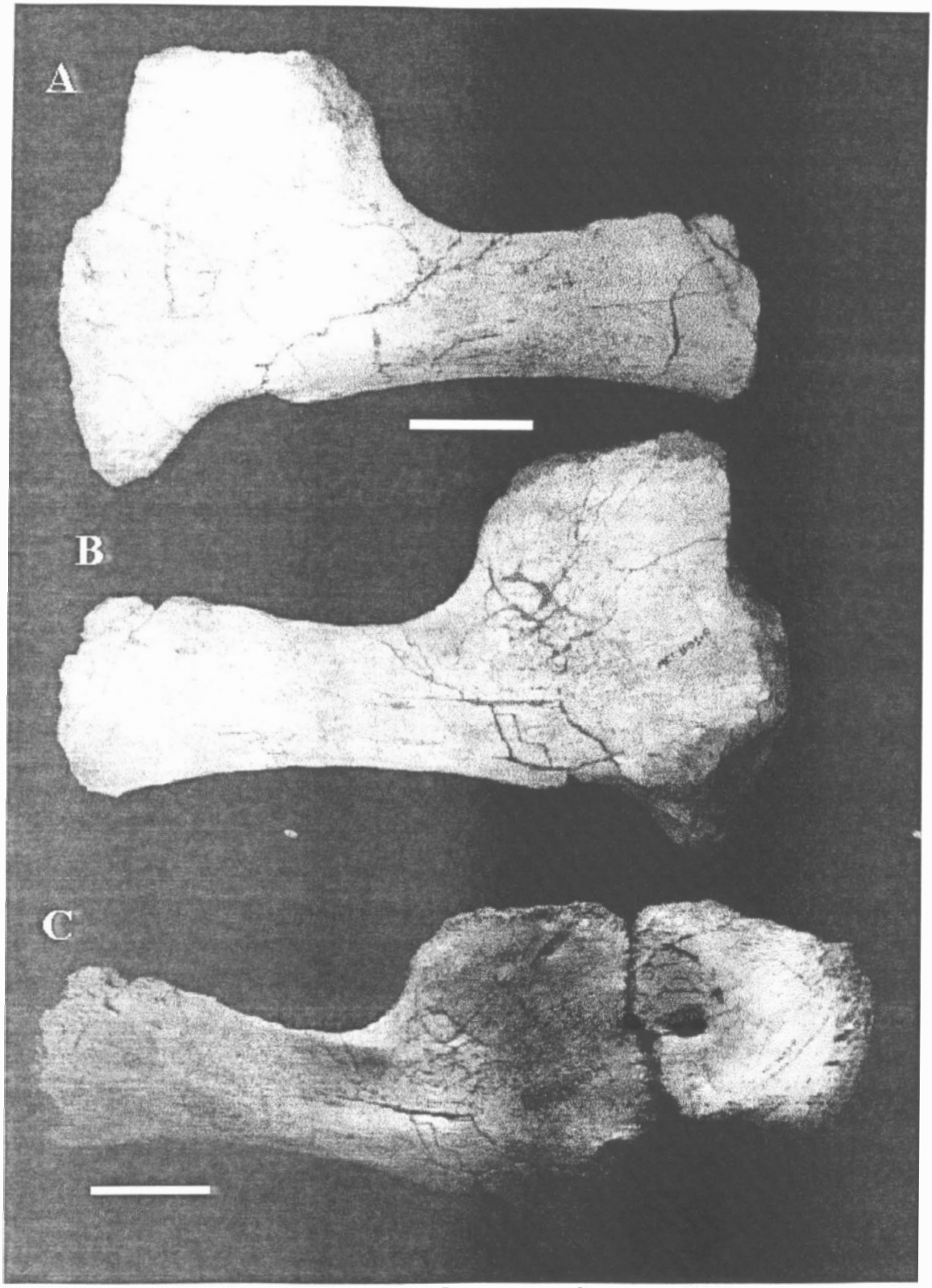


Fig. 49. Left scapula MCT 1691-R in: A) lateral; B) medial and C) medial (with articulated coracoid) views. Scale bar = 10 cm.

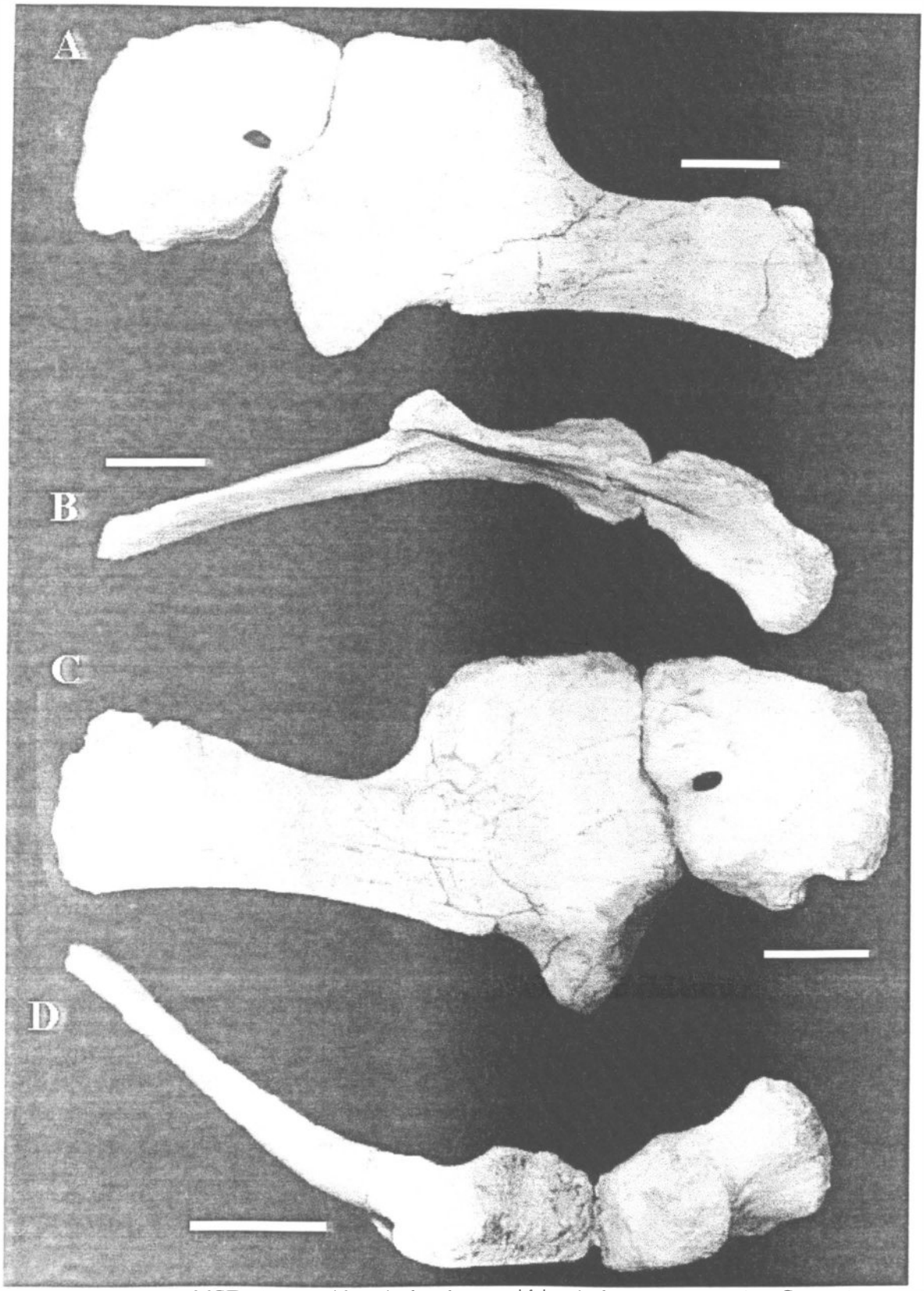


Fig. 50. Left scapula MCT 1691-R with articulated coracoid in; A) lateral; B) superior; C) medial and D) inferior (glenoidal) views. Scale bar = 10 cm.

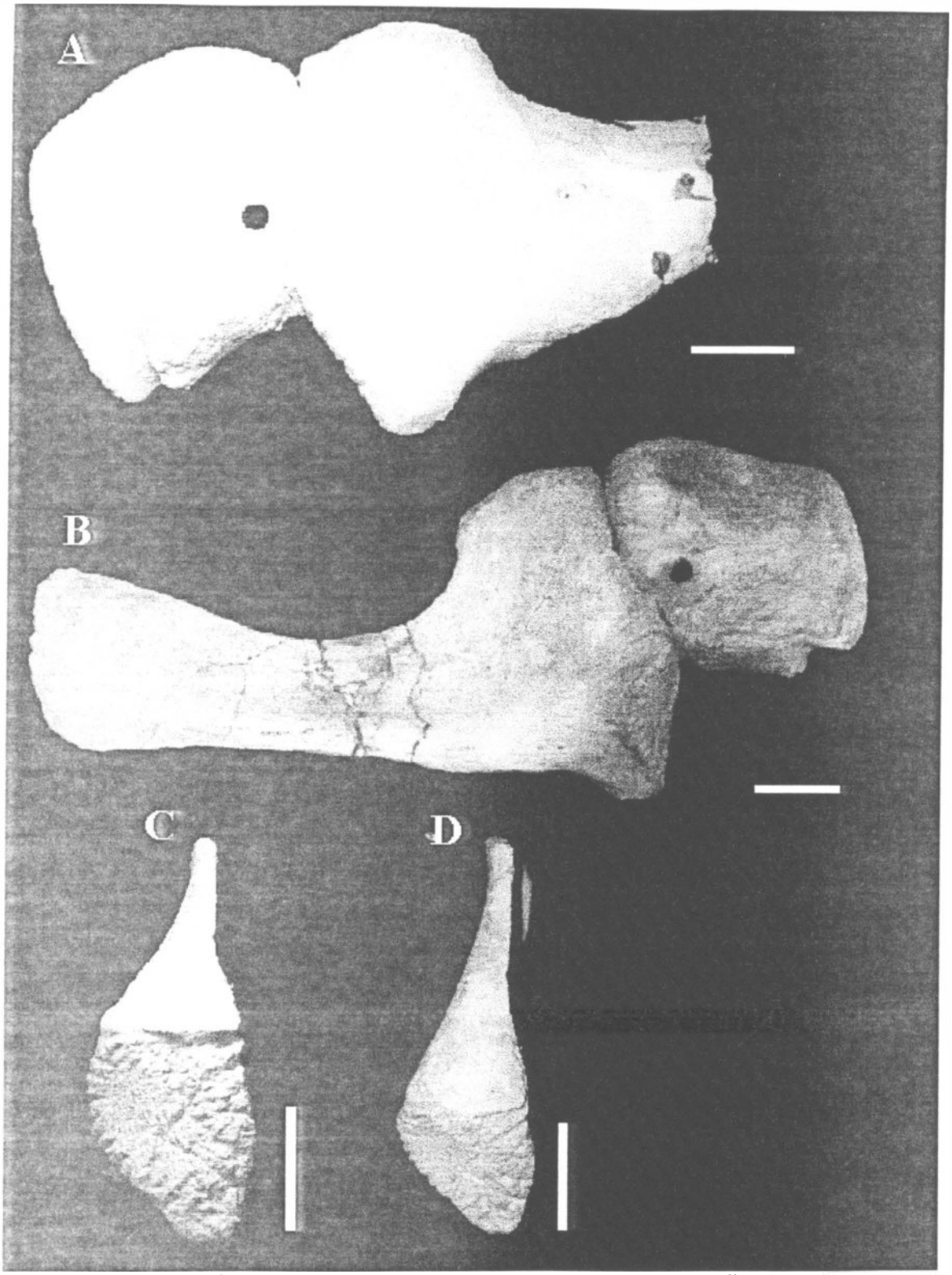


Fig. 51. Left scapula MCT 1703-R with articulated coracoid in: A) lateral; B) medial views. Left scapula MCT 1703-R IN C) glenoidal and D) anterior views. Scale bar = 10 cm.

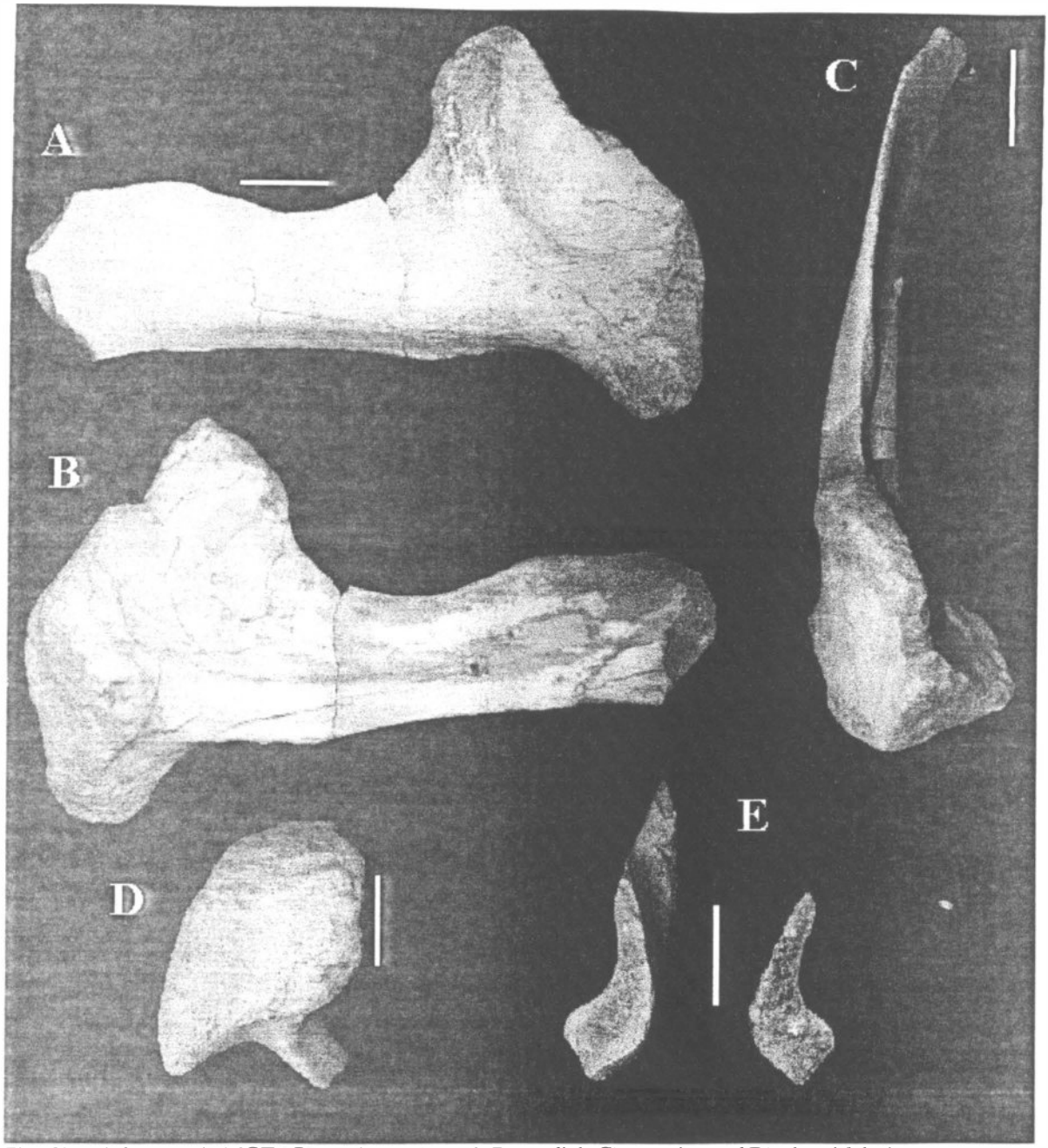


Fig. 52. Right scapula MCT 1708-R in: A) lateral; B) medial; C) superior and D) glenoidal views. E) cross-section, showing "L" shaped profile of the blade. Scale bar = 10 cm.

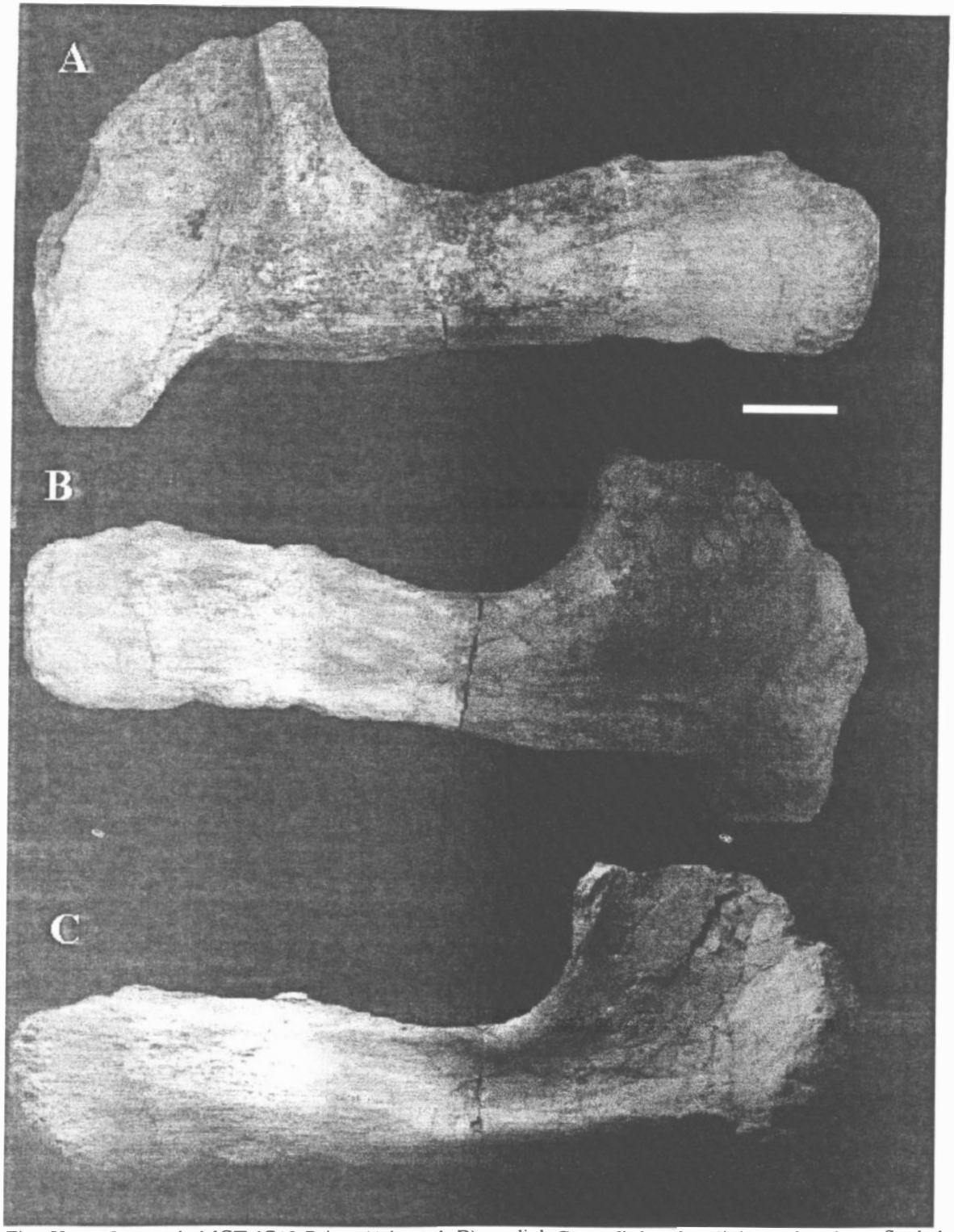


Fig. 53. Left scapula MCT 1709-R in: A) lateral; B) medial; C) medial (at low light angle) views. Scale bar = 10 cm.

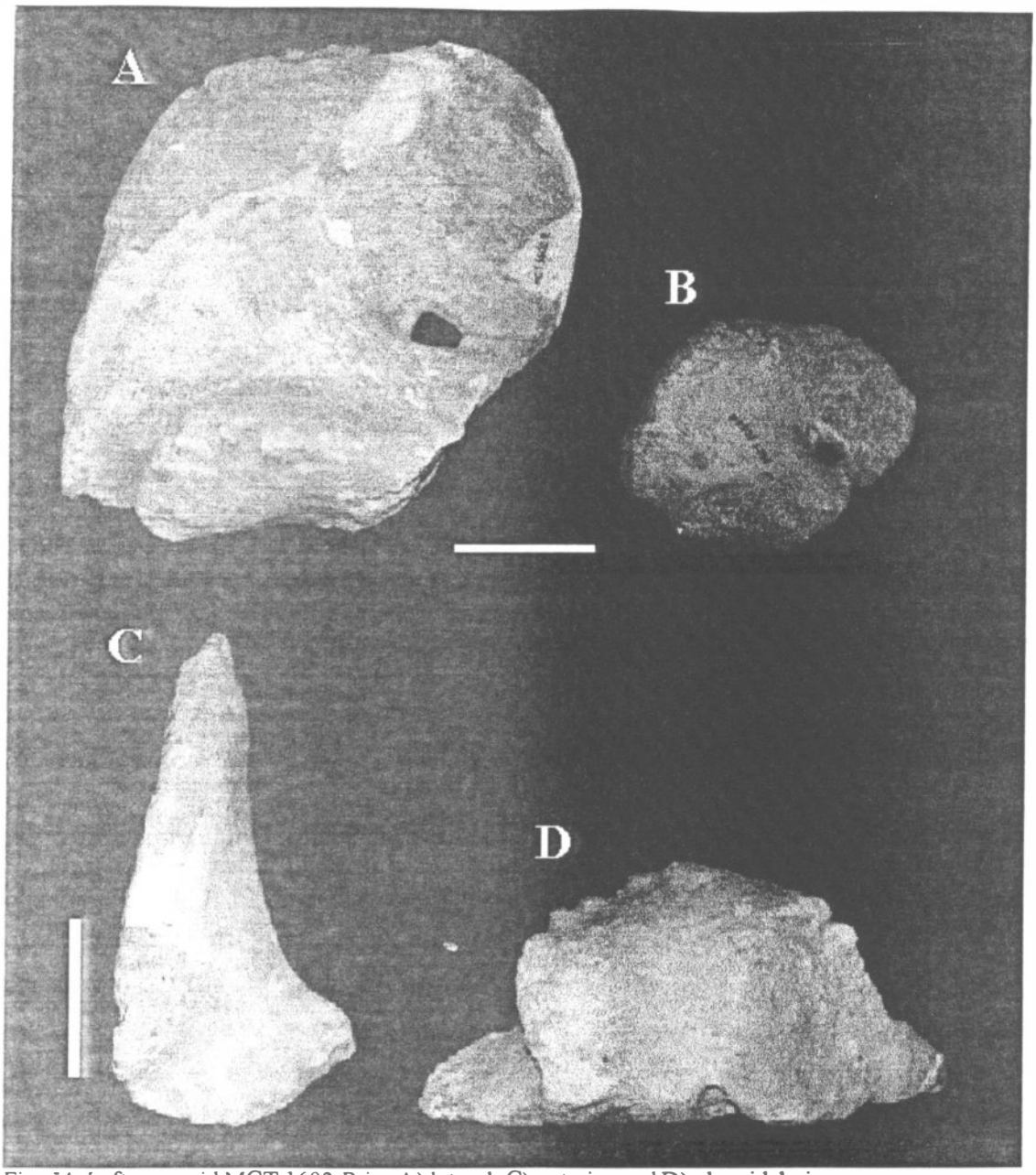


Fig. 54. Left coracoid MCT 1602-R in: A) lateral, C) anterior and D) glenoidal views.
B) Left coracoid MCT 1653-R in lateral view, for size comparison (A and B at the same scale). Scale bar = 10 cm.

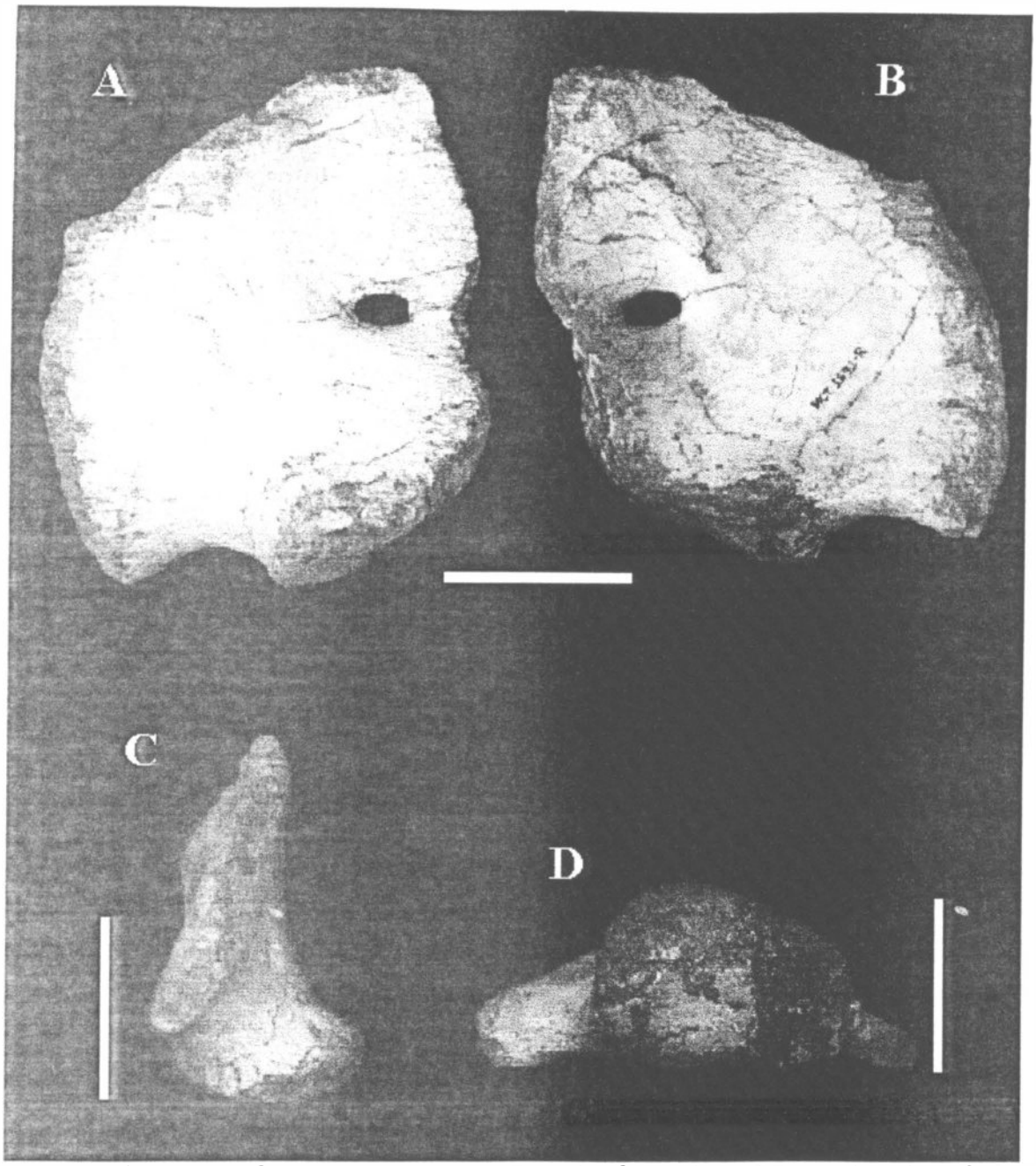


Fig. 55. Left coracoid MCT 1691-R in: A) lateral, B) medial; C) anterior and D) glenoidal views. Scale bar = 10 cm.

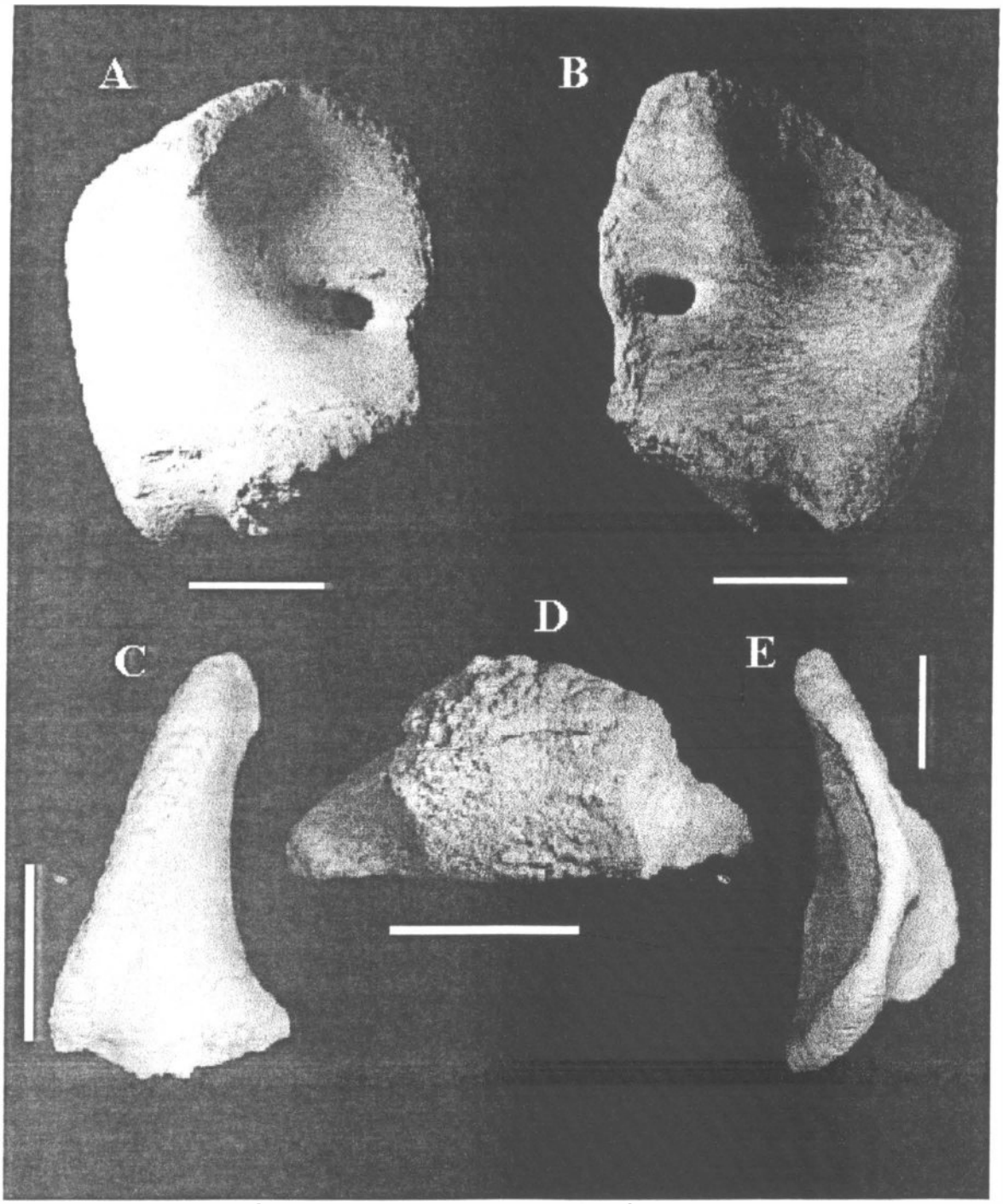


Fig. 56. Left coracoid MCT 1703-R in: A) lateral; B) medial; C) anterior; D) glenoidal and E) superior views. Scale bar = 10 cm.

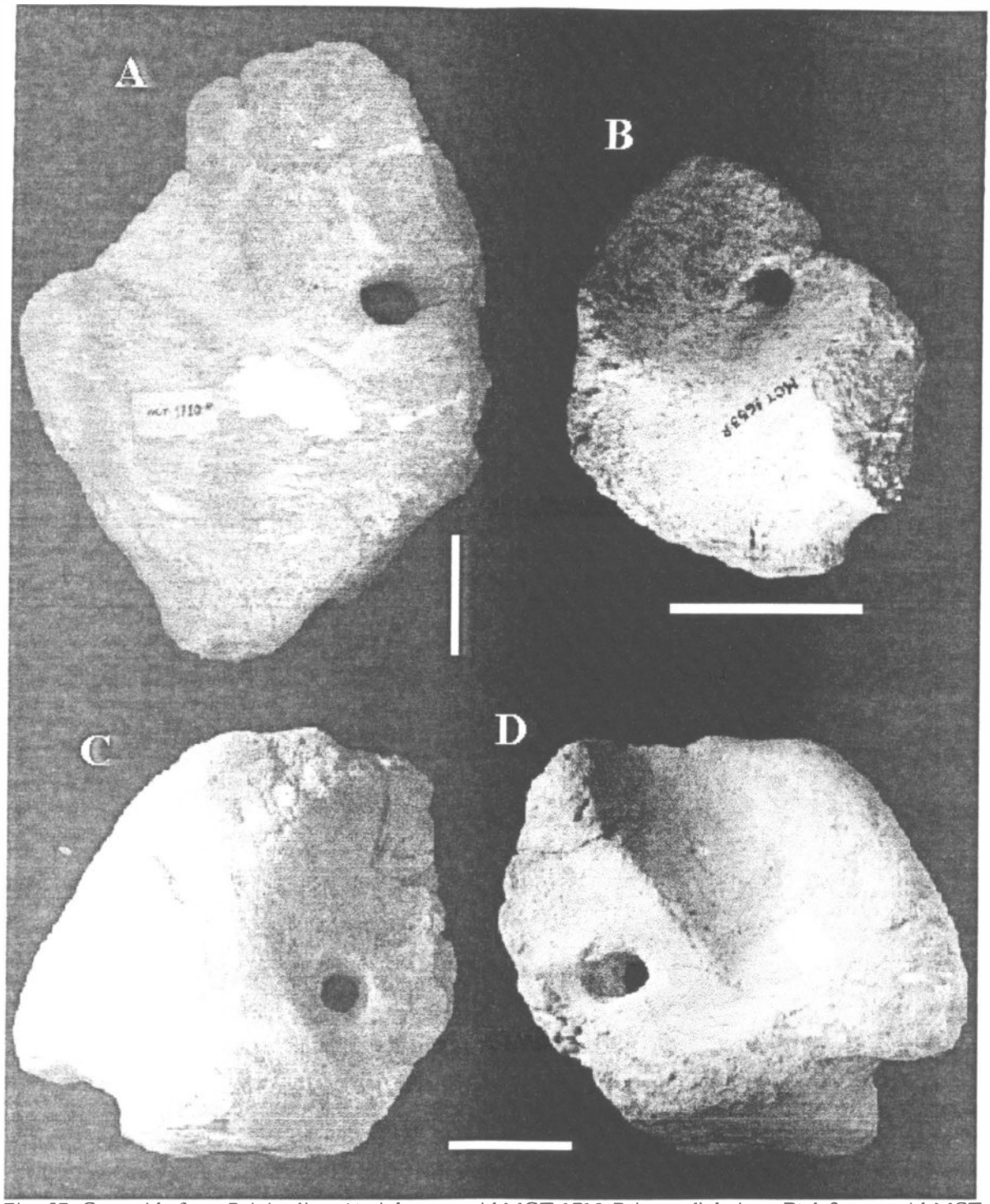


Fig. 57. Coracoids from Peirópolis: A) right coracoid MCT 1710-R in medial view; B) left coracoid MCT 1653-R in lateral view.

Left coracoid MCT 1600-R in C) lateral and D) medial views. Scale bar = 10 cm.

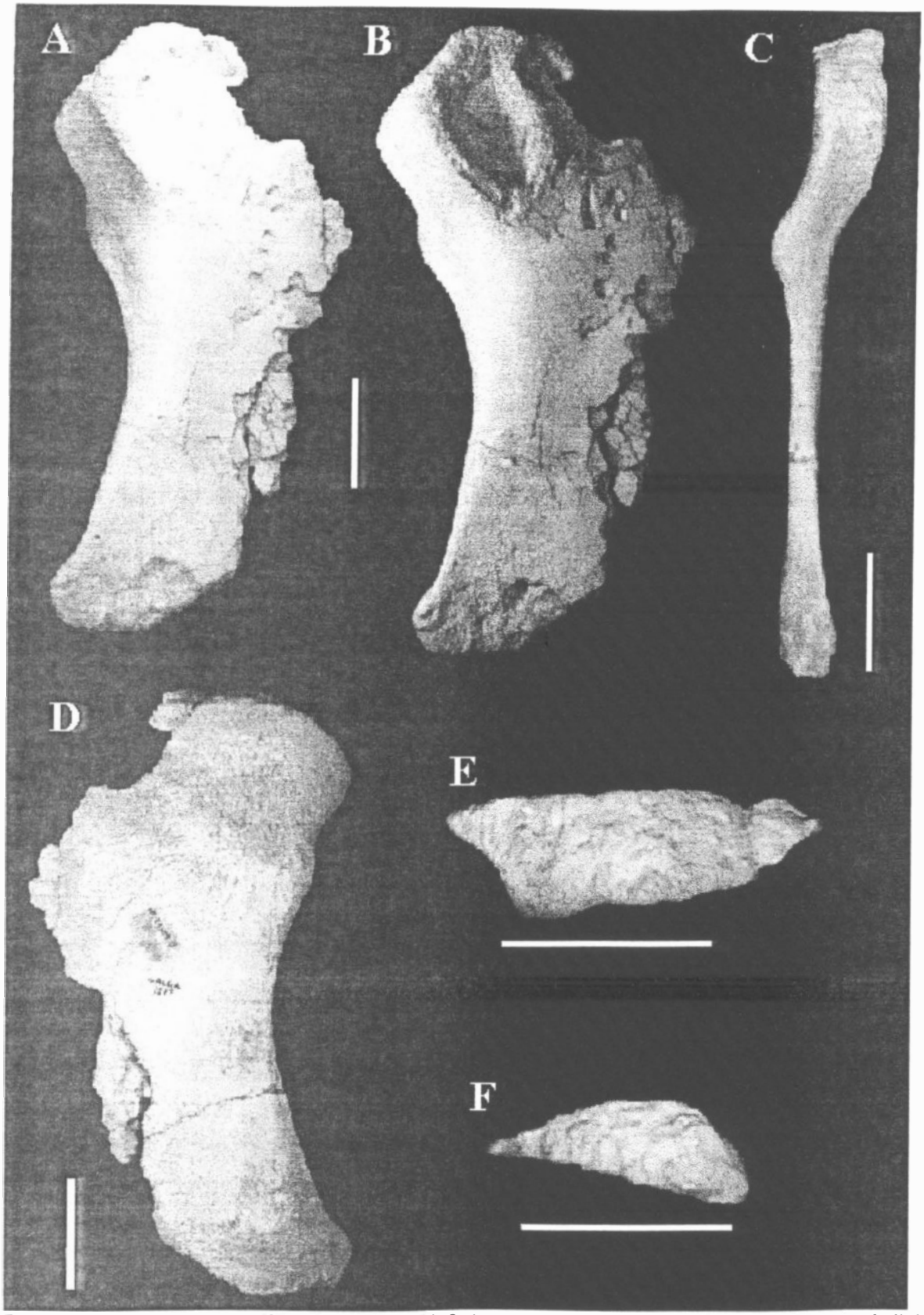


Fig. 58. Right sternal plate MCT 1589-R in: A) inferior or ventral (light from the right); B) ventral (light from the left); C) lateral; D) superior or visceral; E) anterior and F) posterior views. In C, ventral surface faces right; in E and F, ventral surface faces down. Scale bar = 10 cm.

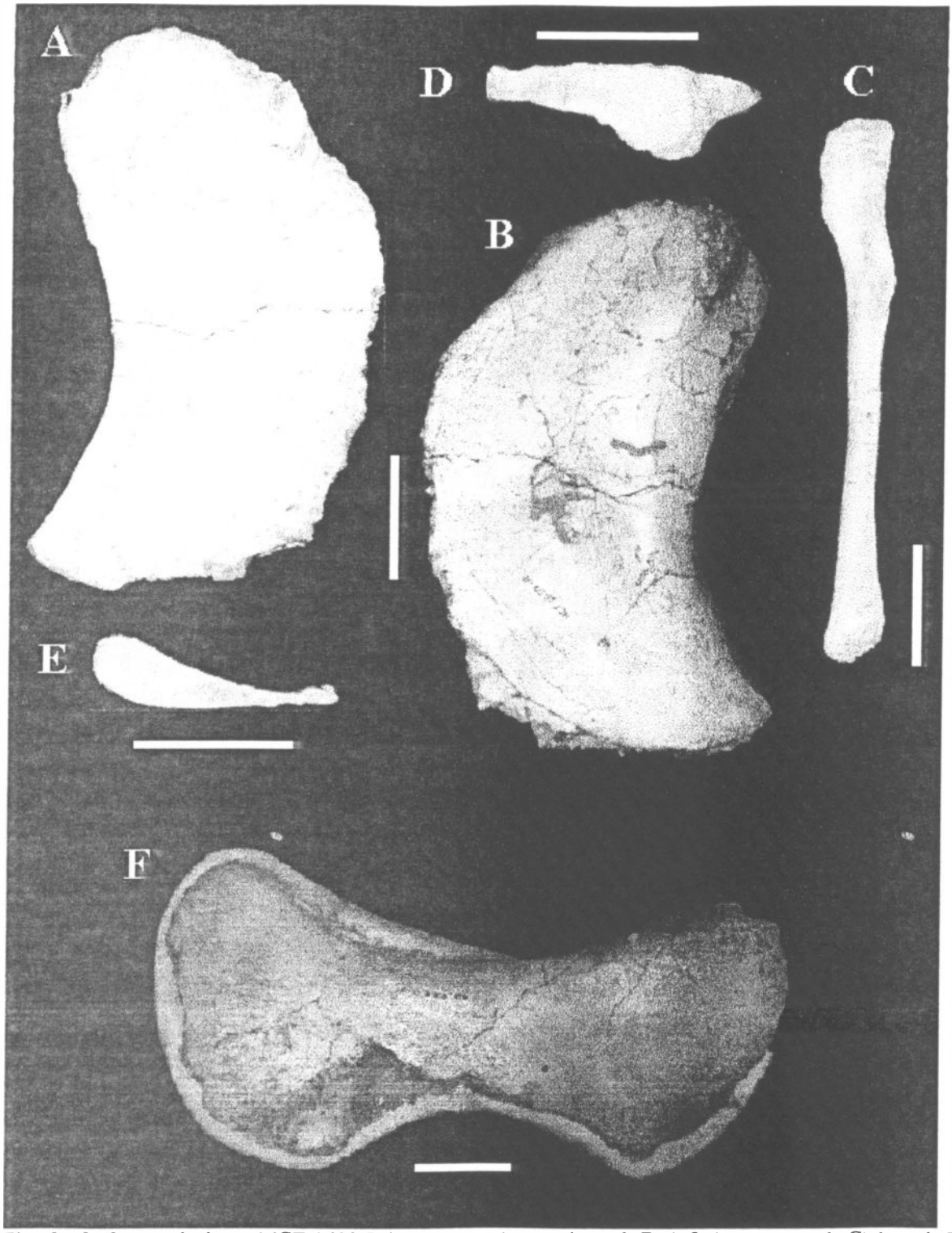


Fig. 59. Left sternal plate. MCT 1690-R in: A) superior or visceral; B) inferior or ventral; C) lateral; D) anterior and E) posterior views. In C, ventral surface faces right; in D and E, ventral surface faces down. F) Left sternal Fig. MCT 1698-R in superior view. Scale bar = 10 cm.

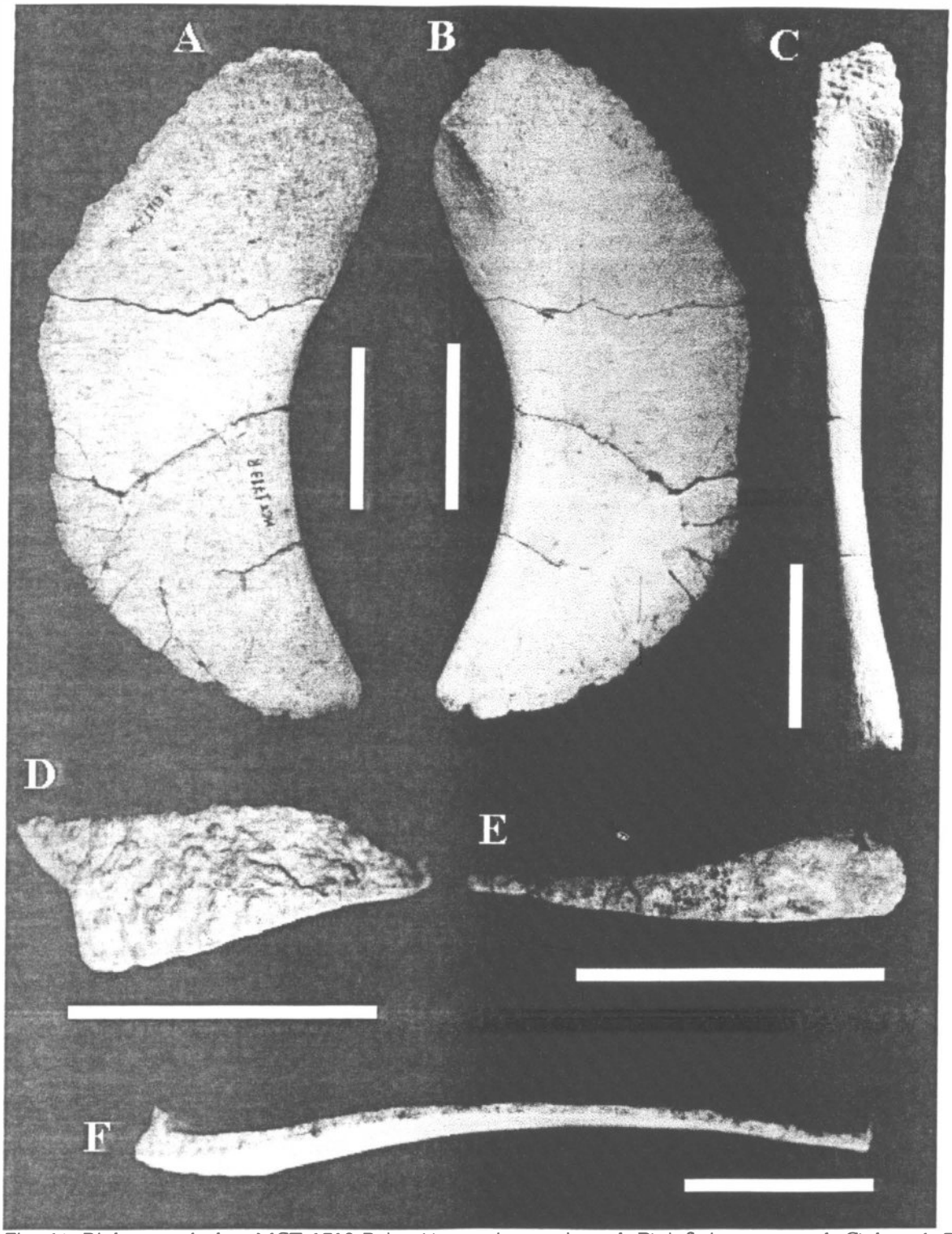


Fig. 60. Right sternal plate MCT 1713-R in: A) superior or visceral; B) inferior or ventral; C) lateral; D) anterior; E) posterior and F) medial views. In C, ventral surface faces right; in D, E and F, ventral surface faces down. Scale bar = 10 cm.

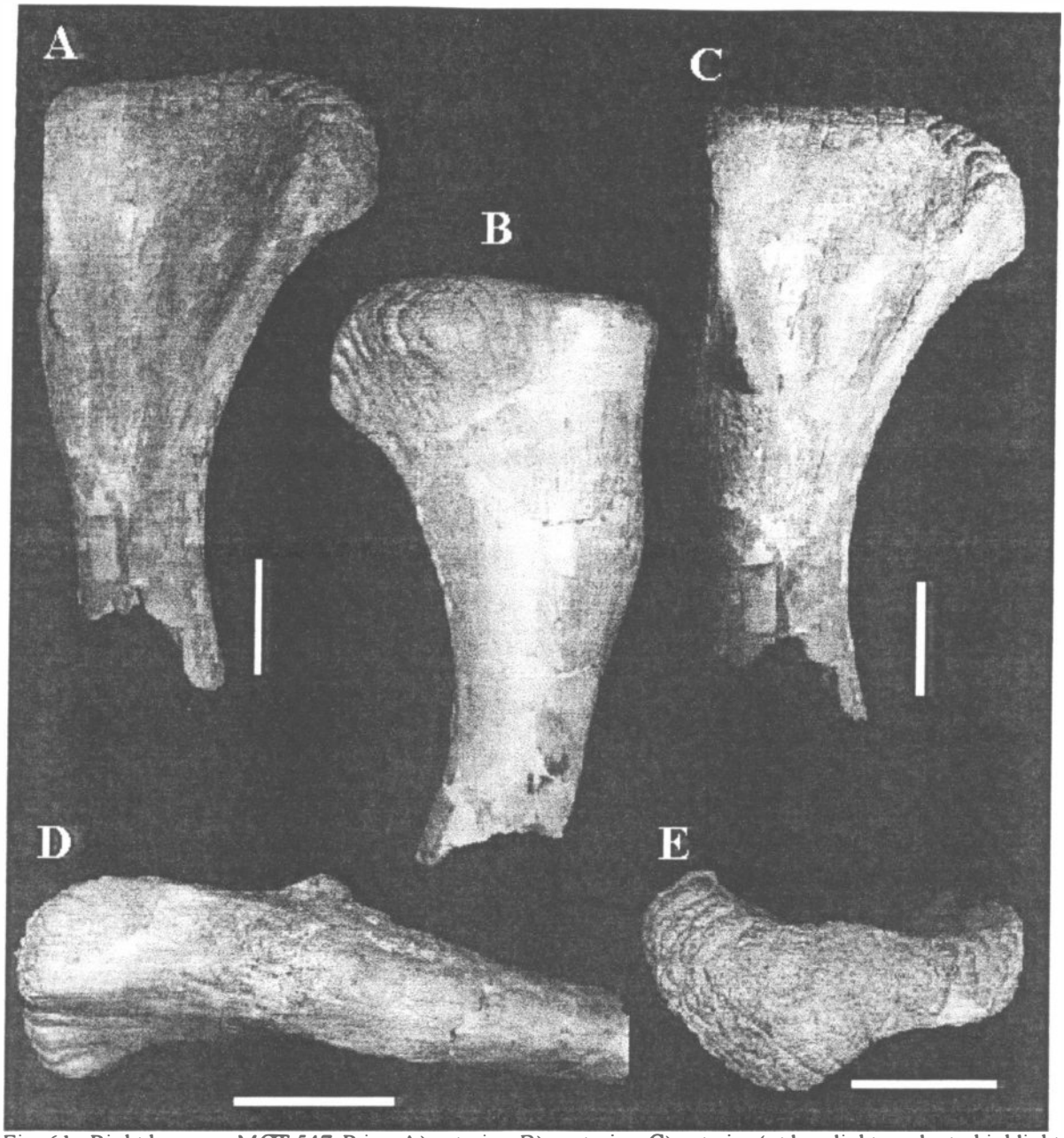


Fig. 61. Right humerus MCT 547-R in: A) anterior; B) posterior; C) anterior (at low light angle, to highlight the prominence over deltopectoral crest); D) lateral and E) proximal views. Scale bar = 10 cm.

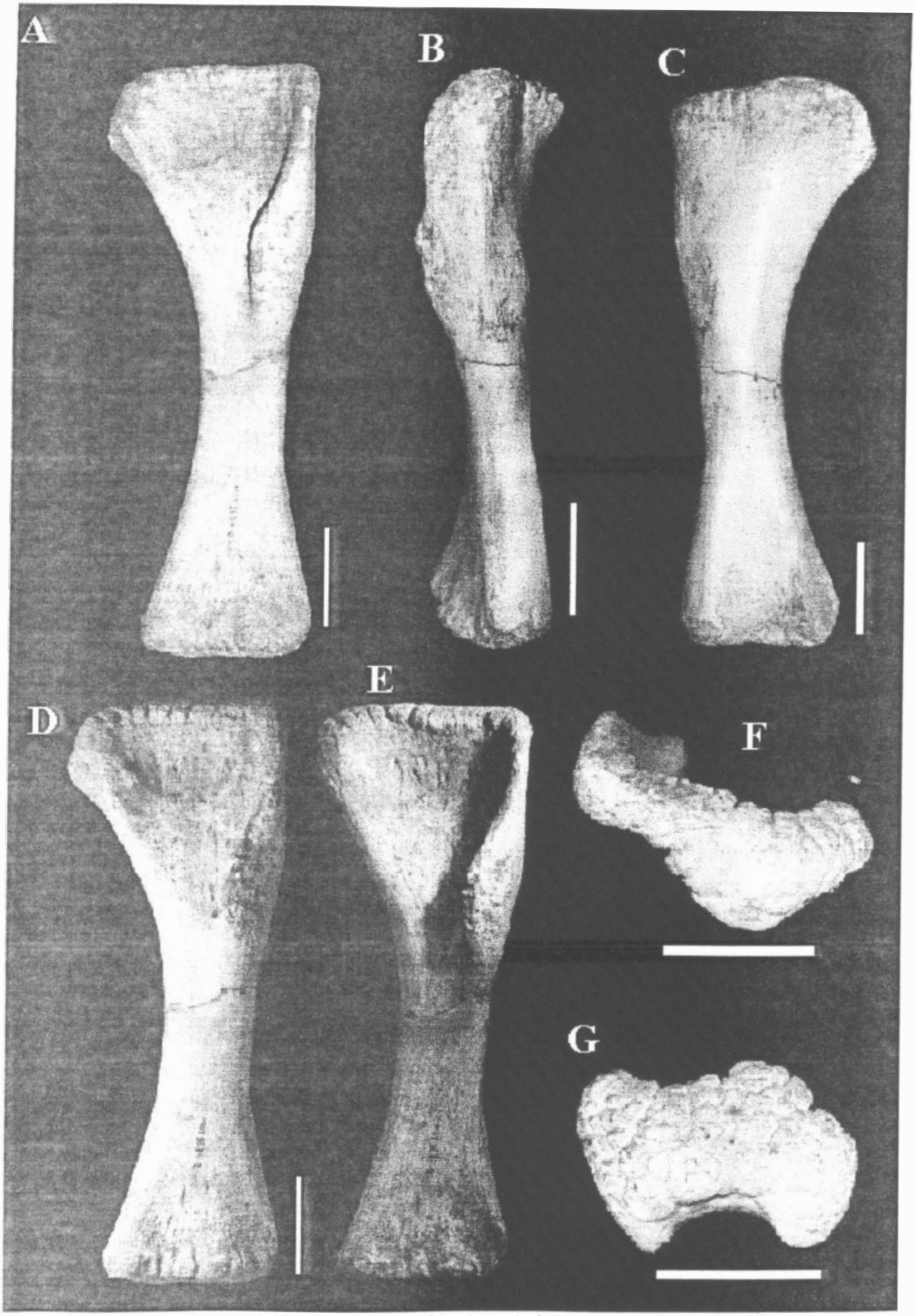


Fig. 62. Left humerus MCT 1674-R in: A) anterior; B) lateral; C) posterior; D) anterior (light from left); E) anterior (light from right); F) proximal and G) distal views. Scale bar = 10 cm.

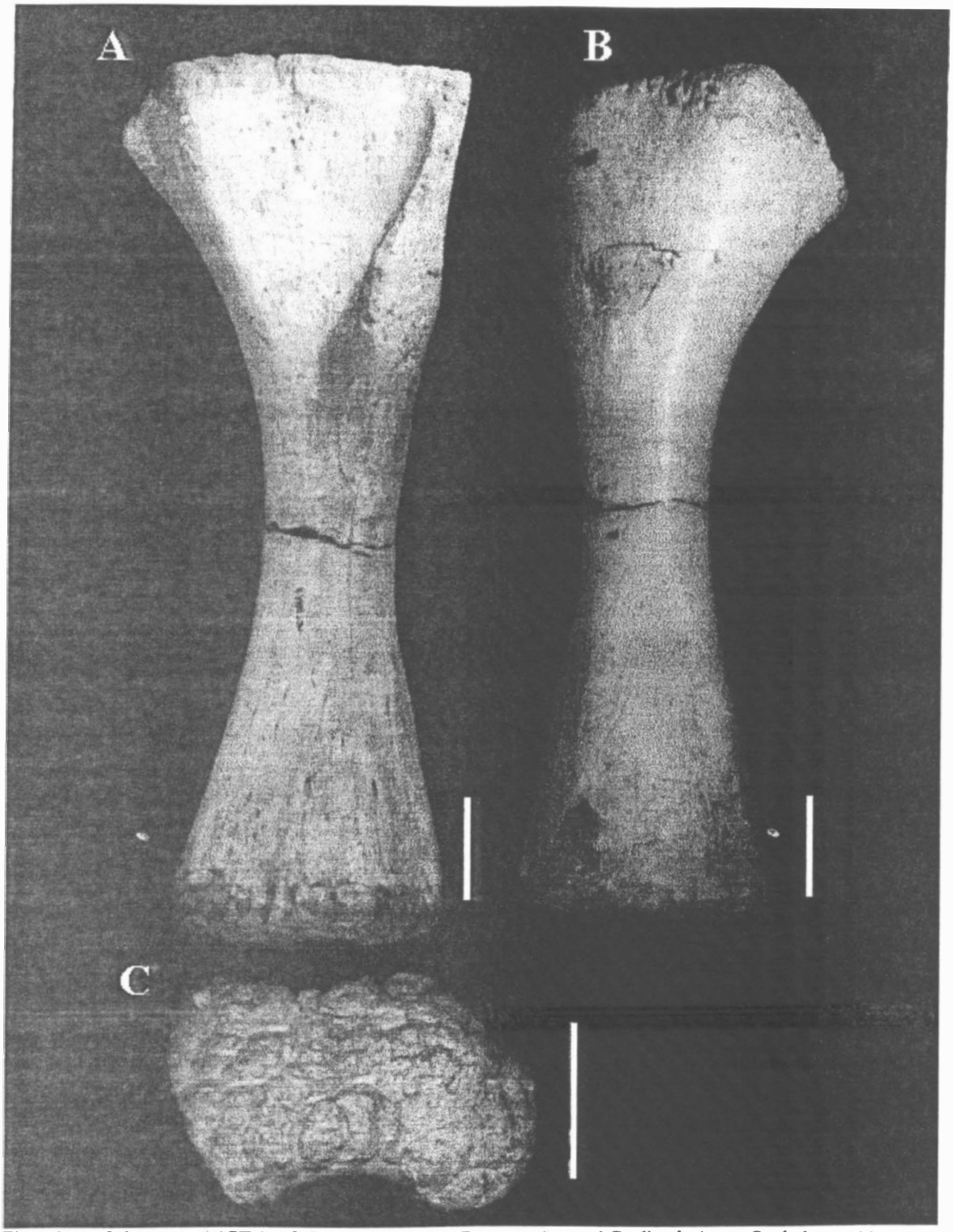


Fig. 63. Left humerus MCT 1682-R in A) anterior; B) posterior and C) distal views. Scale bar = 10 cm.

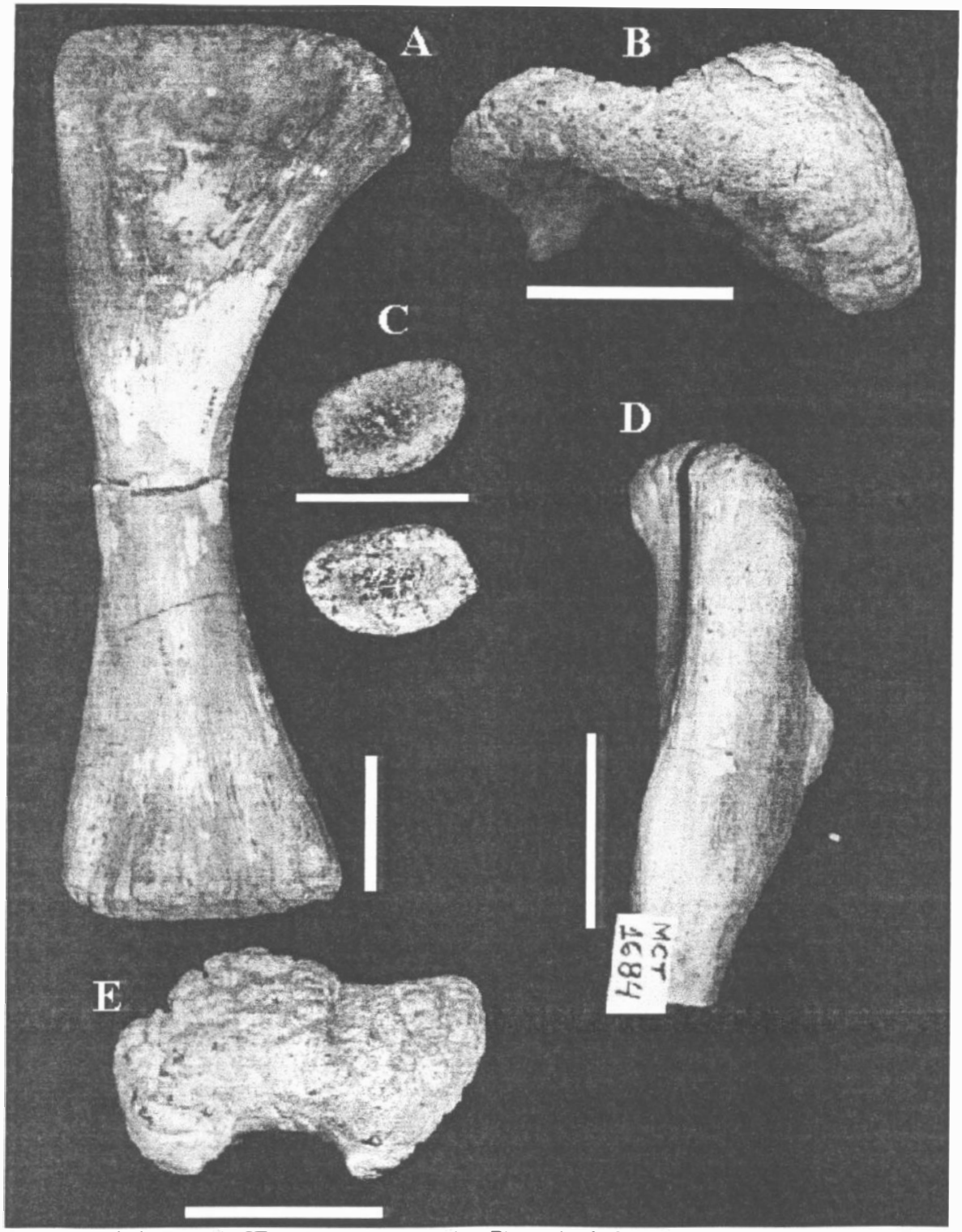


Fig. 64. Right humerus MCT 1684-R in: A) anterior; B) proximal; C) cross-section; D) lateral and E) distal views. Scale bar = 10 cm.

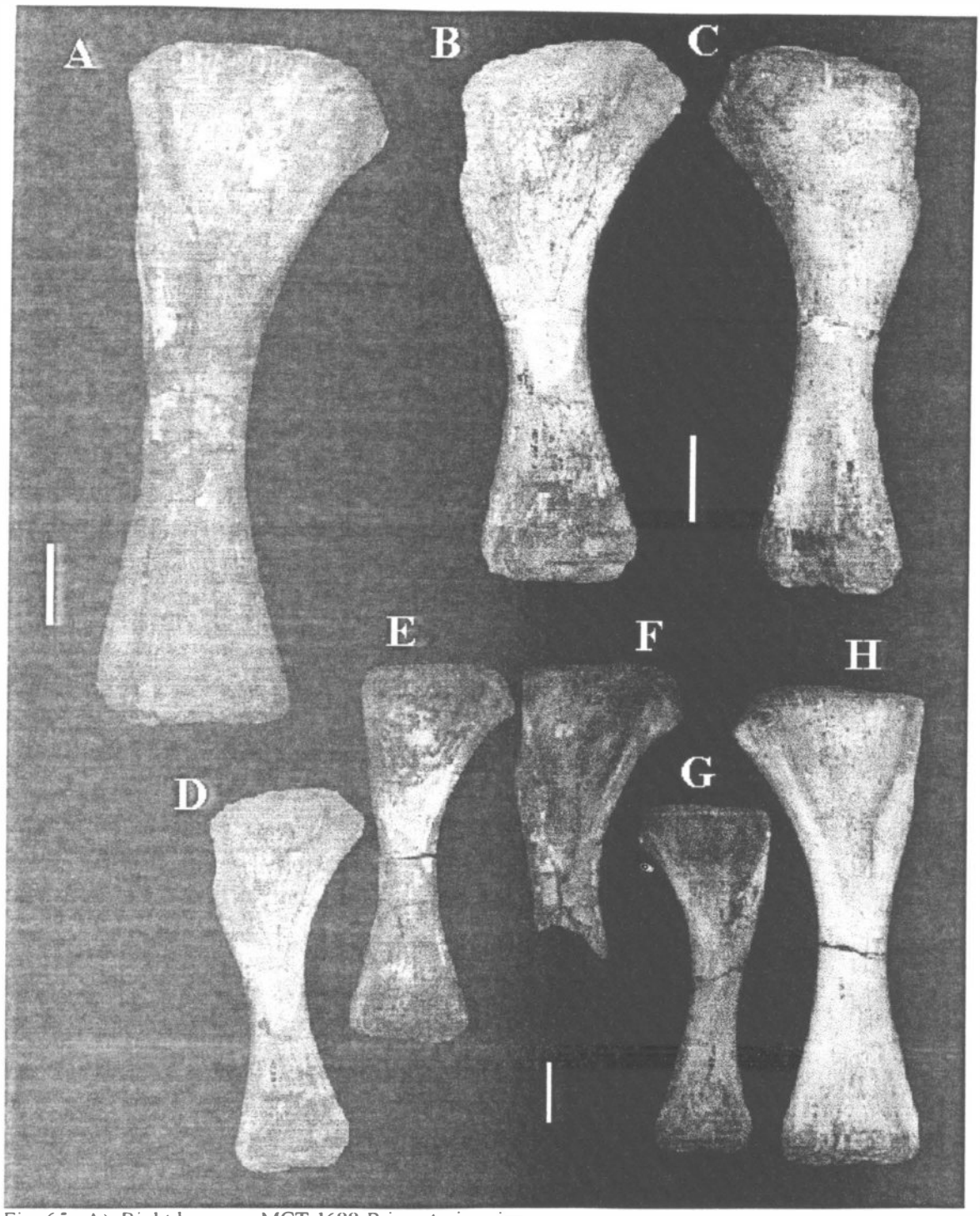


Fig. 65. A) Right humerus MCT 1688-R in anterior view.
Right humerus MCT 1597-R in: B) anterior and C) posterior views.
D to H) humeri from Peirópolis in anterior view: D) MCT 1597-R; E) MCT 1684-R; F) MCT 547-R; G) MCT 1674-R and H) MCT 1682-R. All to the same scale, for size comparison. Scale bar = 10 cm.

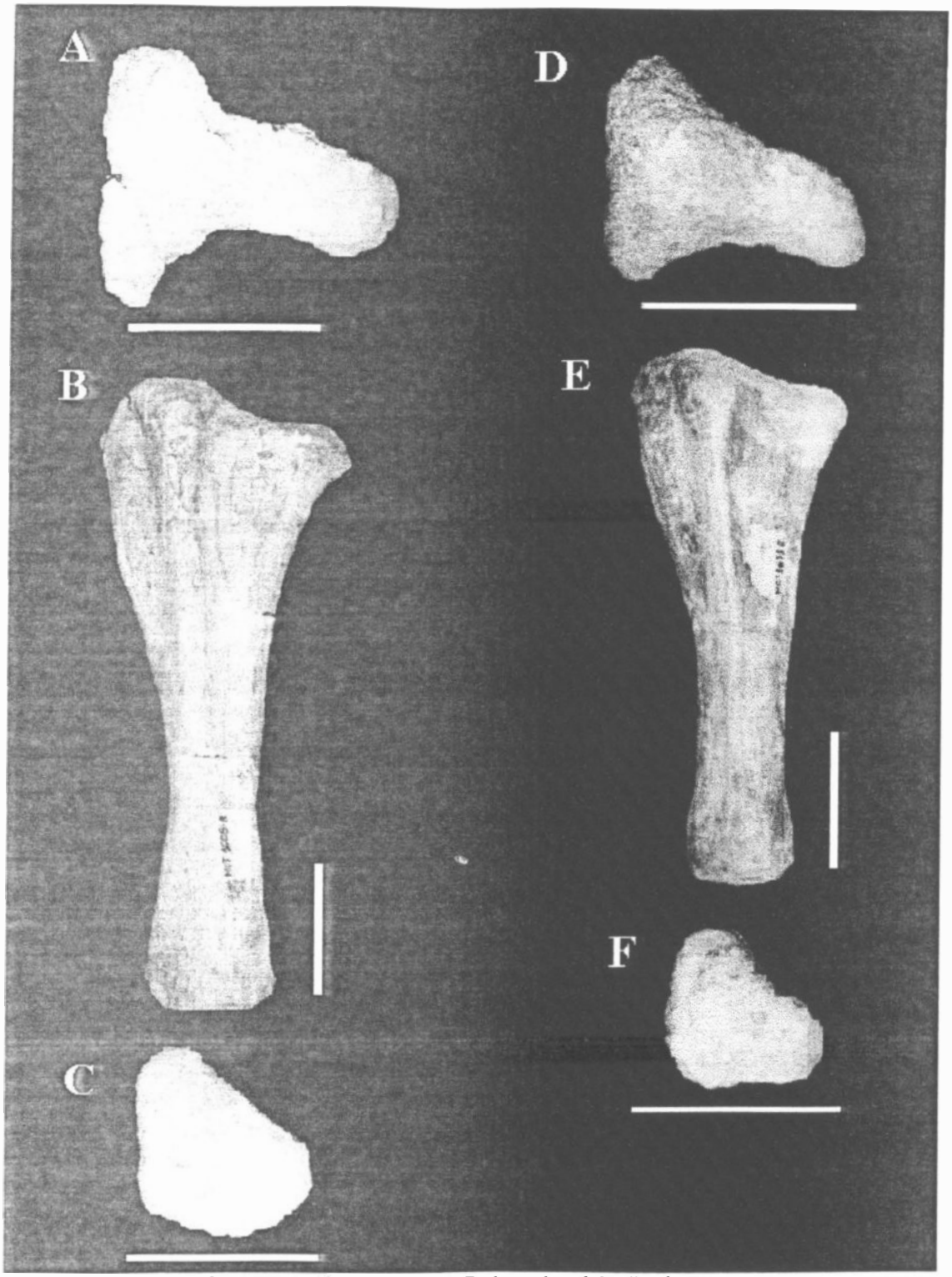


Fig. 66. Right ulna MCT 1609-R in: A) proximal; B) lateral and C) distal views.
Right ulna MCT 1651-R in: D) proximal; E) lateral and F) distal views. Scale bar = 10 cm.

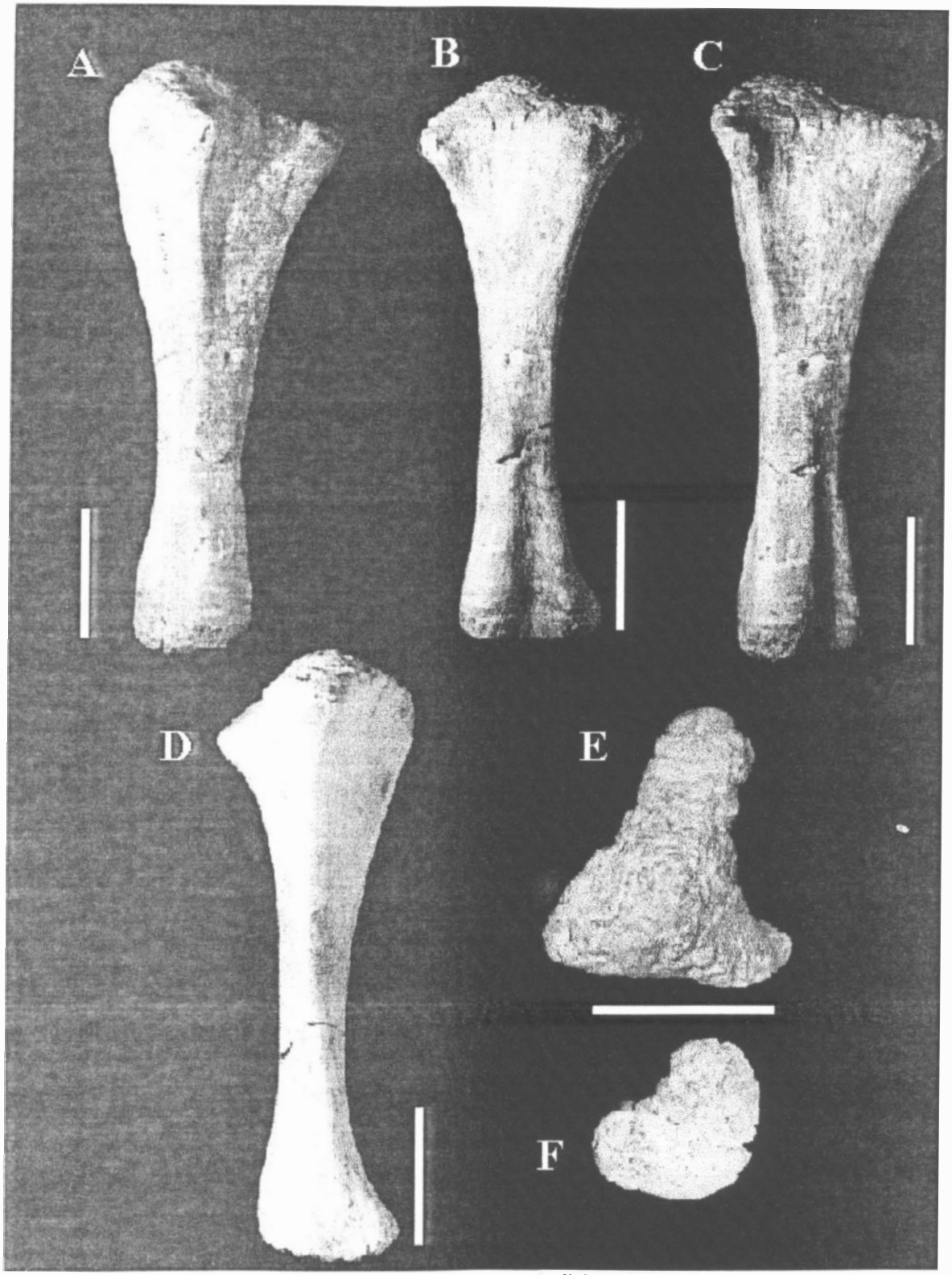


Fig. 67. Right ulna MCT 1659-R in: A) lateral; B) anterior (radial); C) anterior (at slightly different angle); D) medial; E) proximal and F) distal views. Scale bar = 10 cm.

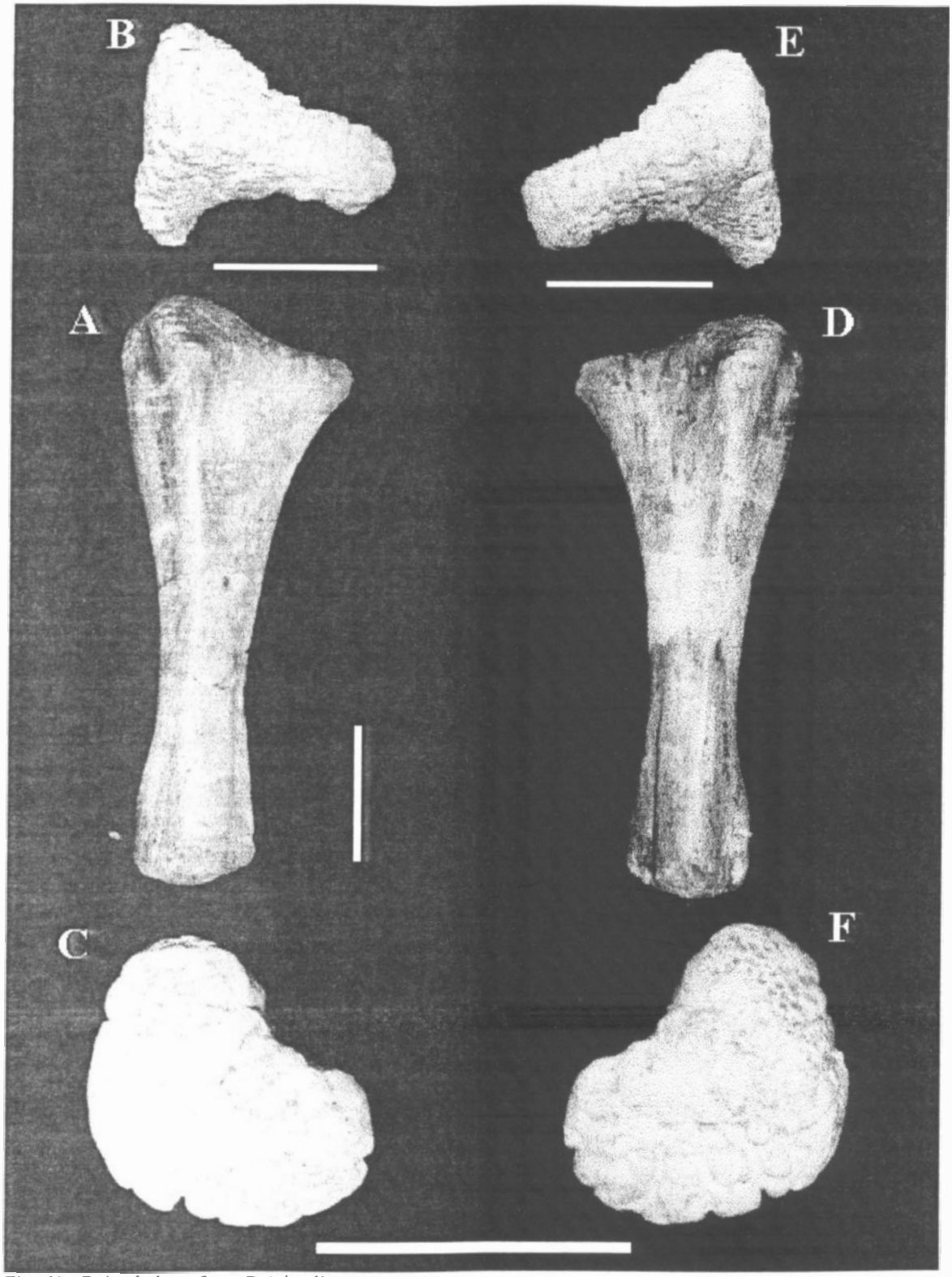


Fig. 68. Paired ulnae from Peirópolis.
Right ulna MCT 1659-R in: A) proximal; B) lateral and C) distal views.
Left ulna MCT 1676-R in: D) proximal; E) lateral and F) distal views. Scale bar = 10 cm.

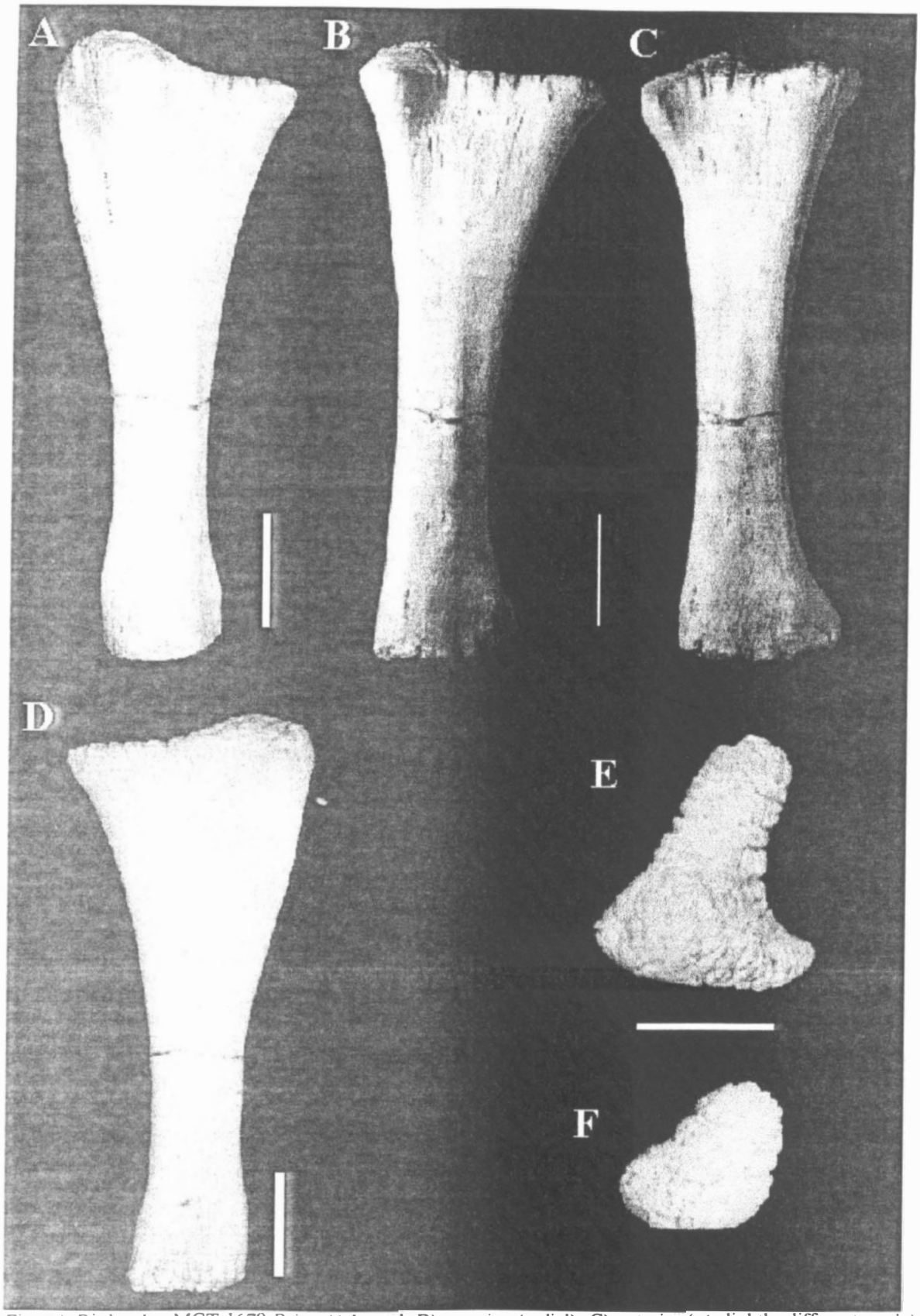


Fig. 69. Right ulna MCT 1678-R in: A) lateral; B) anterior (radial); C) anterior (at slightly different angle); D) medial; E) proximal and F) distal views. Scale bar = 10 cm.

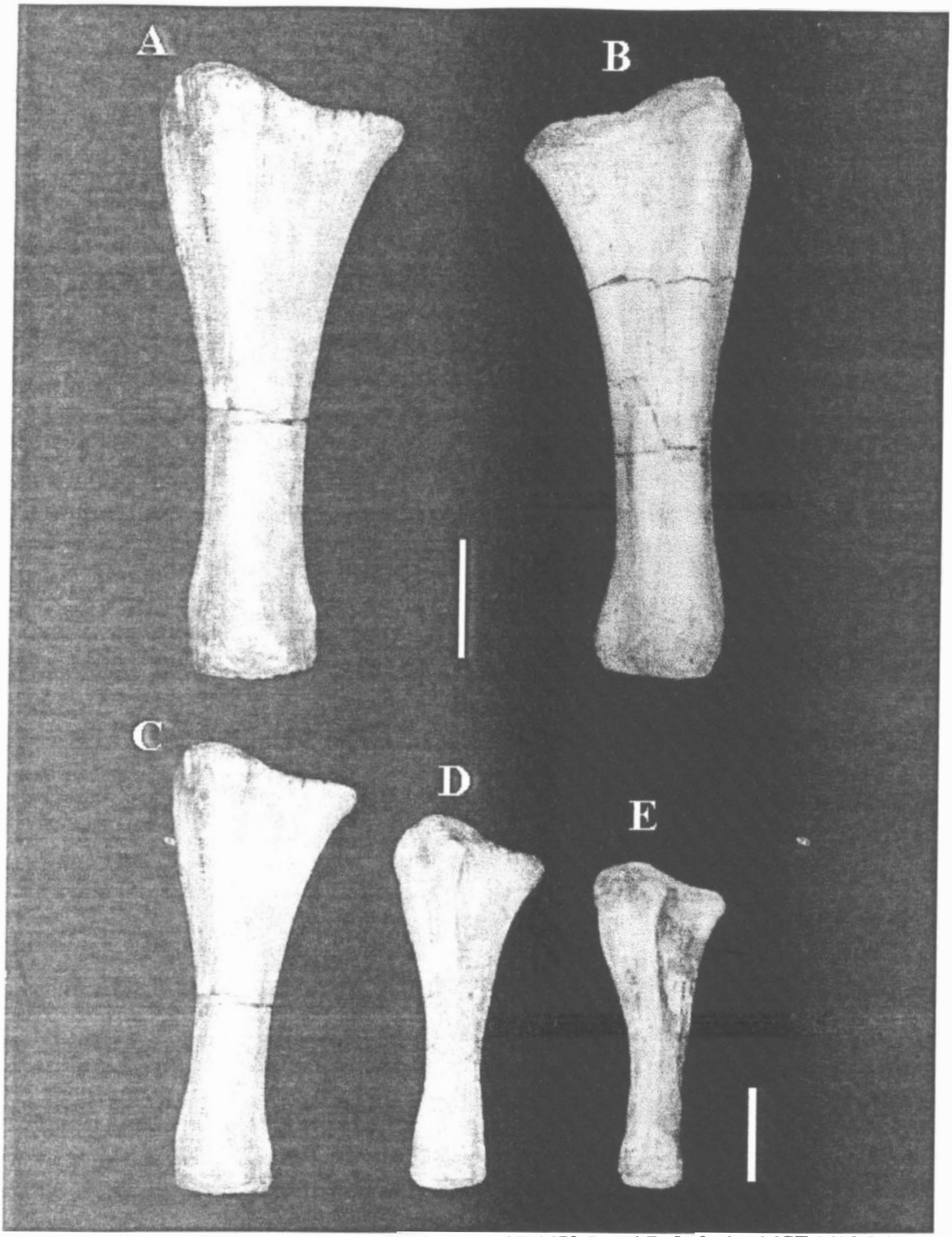


Fig. 70. Paired ulnae from Peirópolis: A) Right ulna MCT 1678-R and B) Left ulna MCT 1635-R in lateral view. Both at same scale.

C to E) Right ulnae for size comparison: C) MCT 1678-R; D) MCT 1659-R and E) MCT 1651-R. All three at same scale. Scale bar = 10 cm.

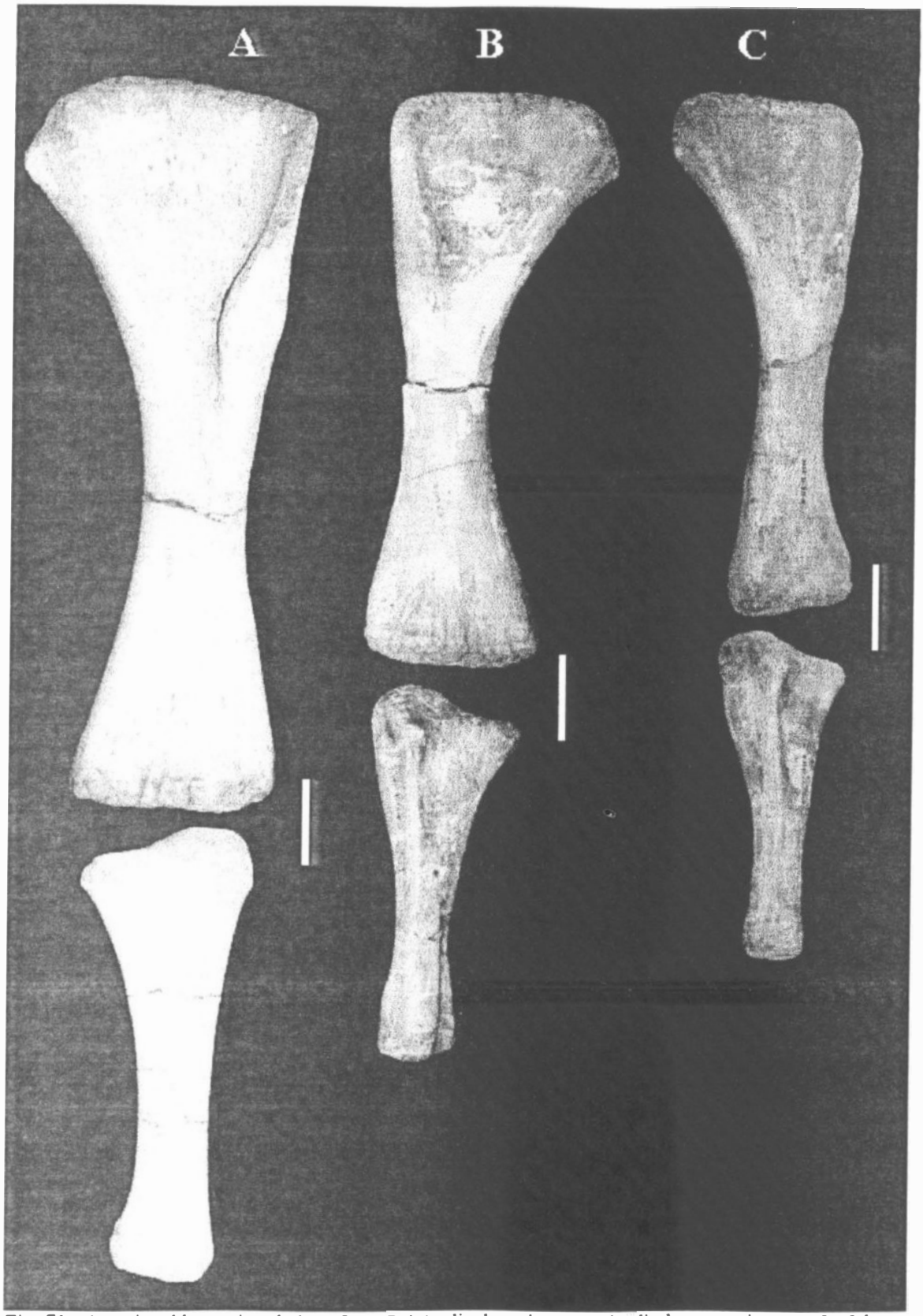


Fig. 71. Associated humeri and ulnae from Peirópolis, based on anterior limb proportions: A) Left humerus MCT 1682-R and left ulna MCT 1635-R; B) Right humerus MCT 1684-R and right ulna MCT 1659-R; C) Left humerus MCT 1674-R and right ulna MCT 1651-R. All three at same scale. Scale bar = 10 cm.

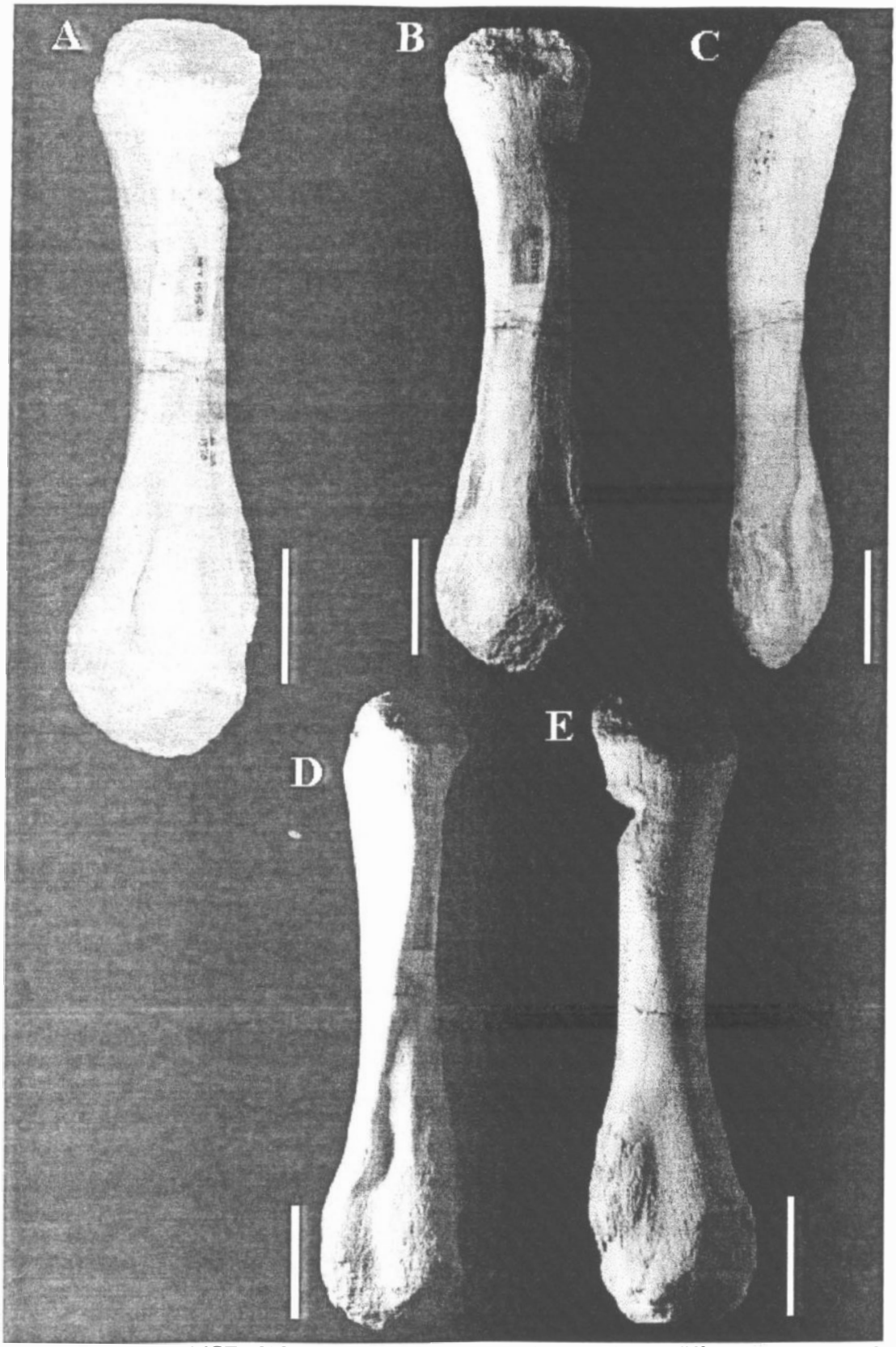


Fig. 72. Right radius MCT 1595-R in: A) posterior (ulnar); B) posterior (at different light angle); C) lateral; D) medio-posterior and E) anterior views. Scale bar = 10 cm.

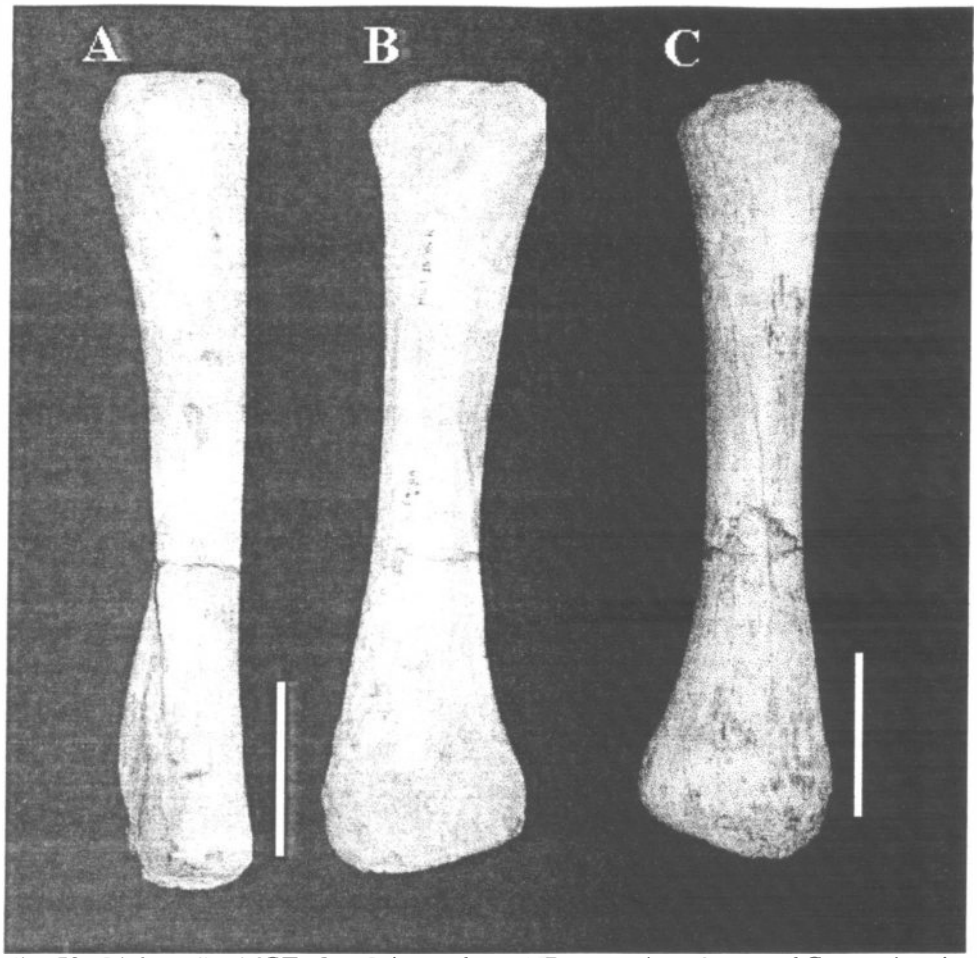


Fig. 73. Right radius MCT 1598-R in: A) lateral; B) posterior (ulnar) and C) anterior views. A and B at same scale. Scale bar = 10 cm.

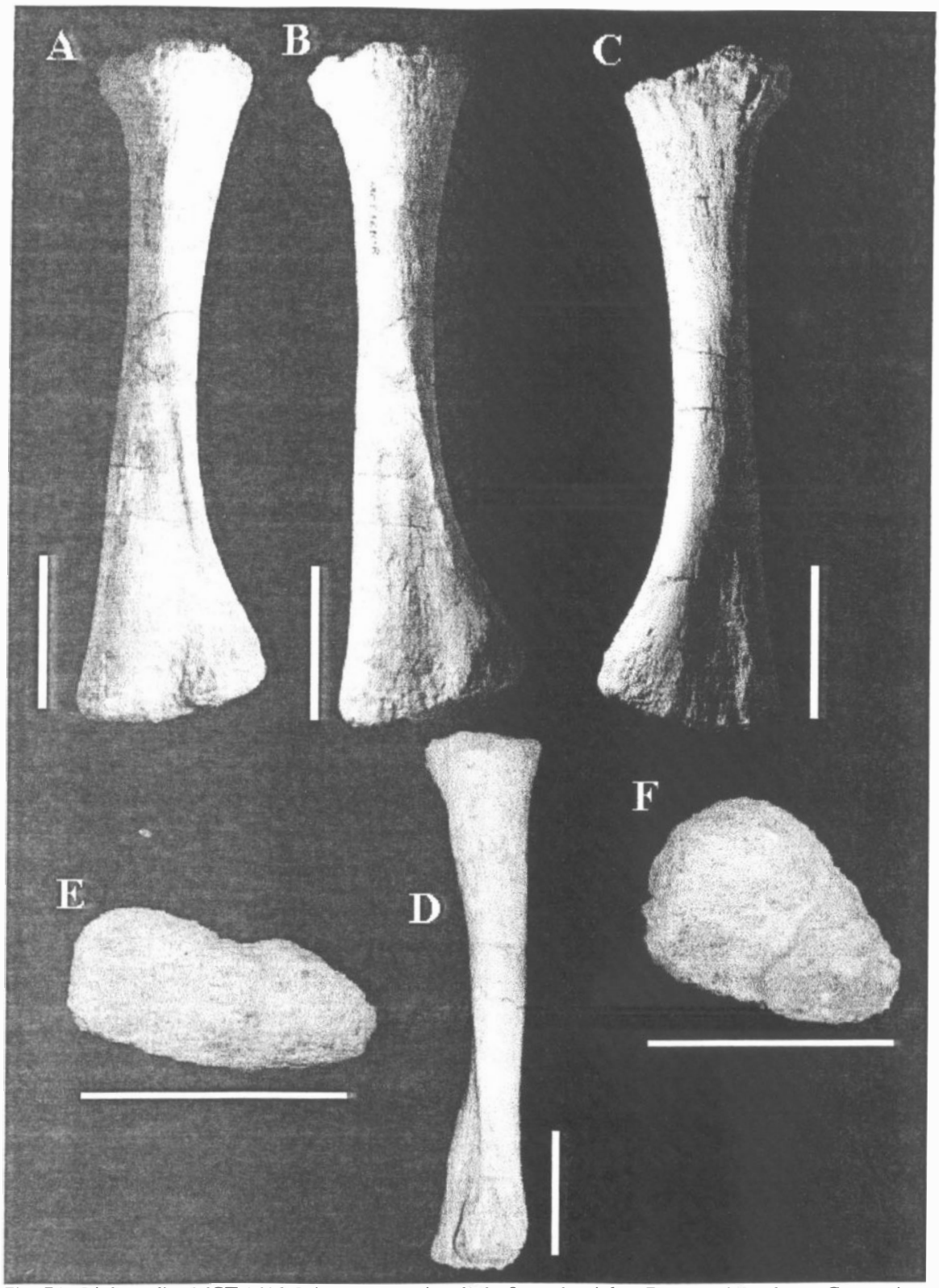


Fig. 74. Right radius MCT 1610-R in: A) posterior (light from the right); B) posterior (ulnar); C) anterior; D) lateral; E) distal and F) proximal views. Scale bar = 10 cm.

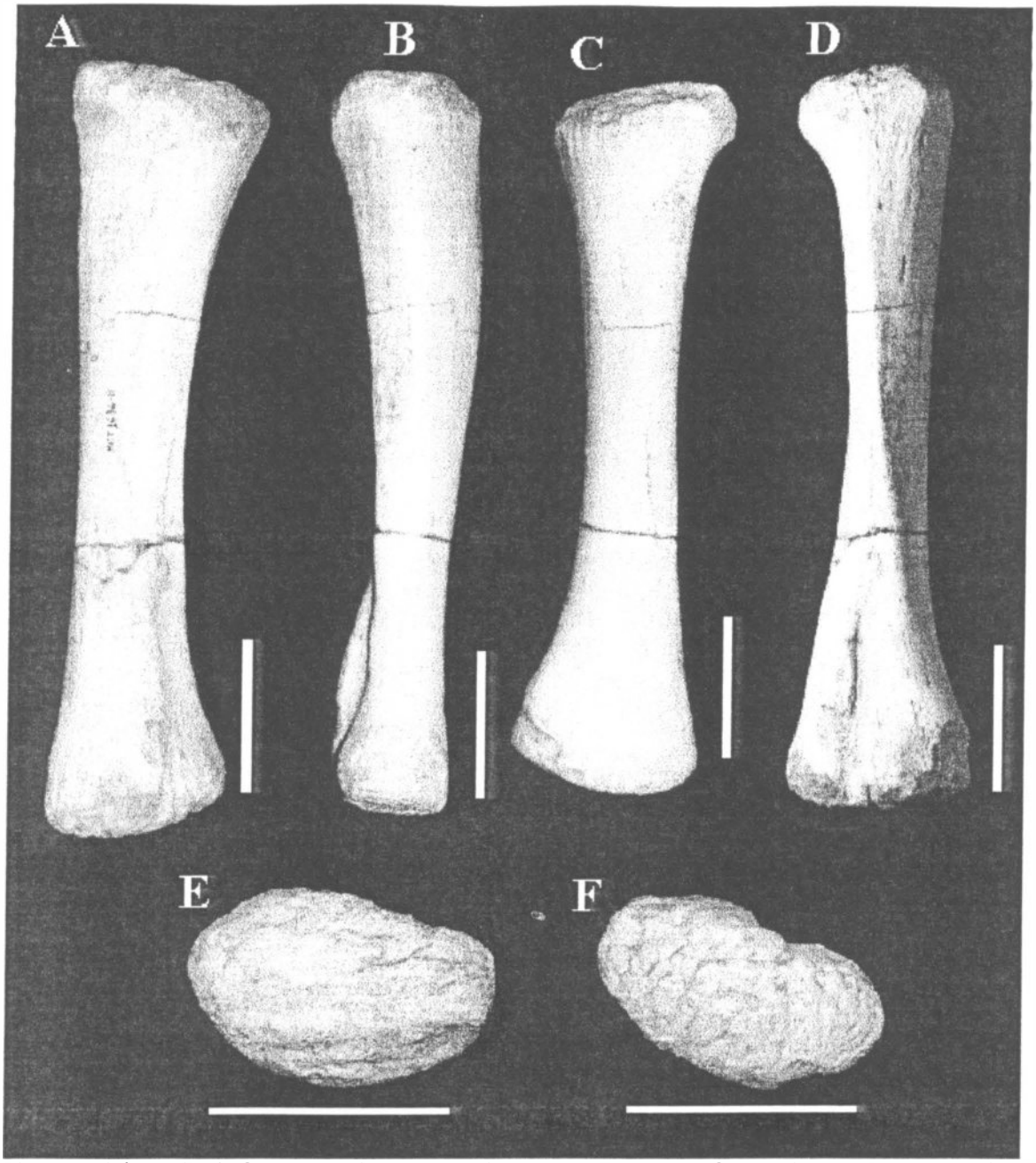


Fig. 75. Right radius MCT 1636-R in: A) posterior (ulnar); B) lateral; C) anterior; D) latero-posterior; E) proximal and F) distal views. Scale bar = 10 cm.

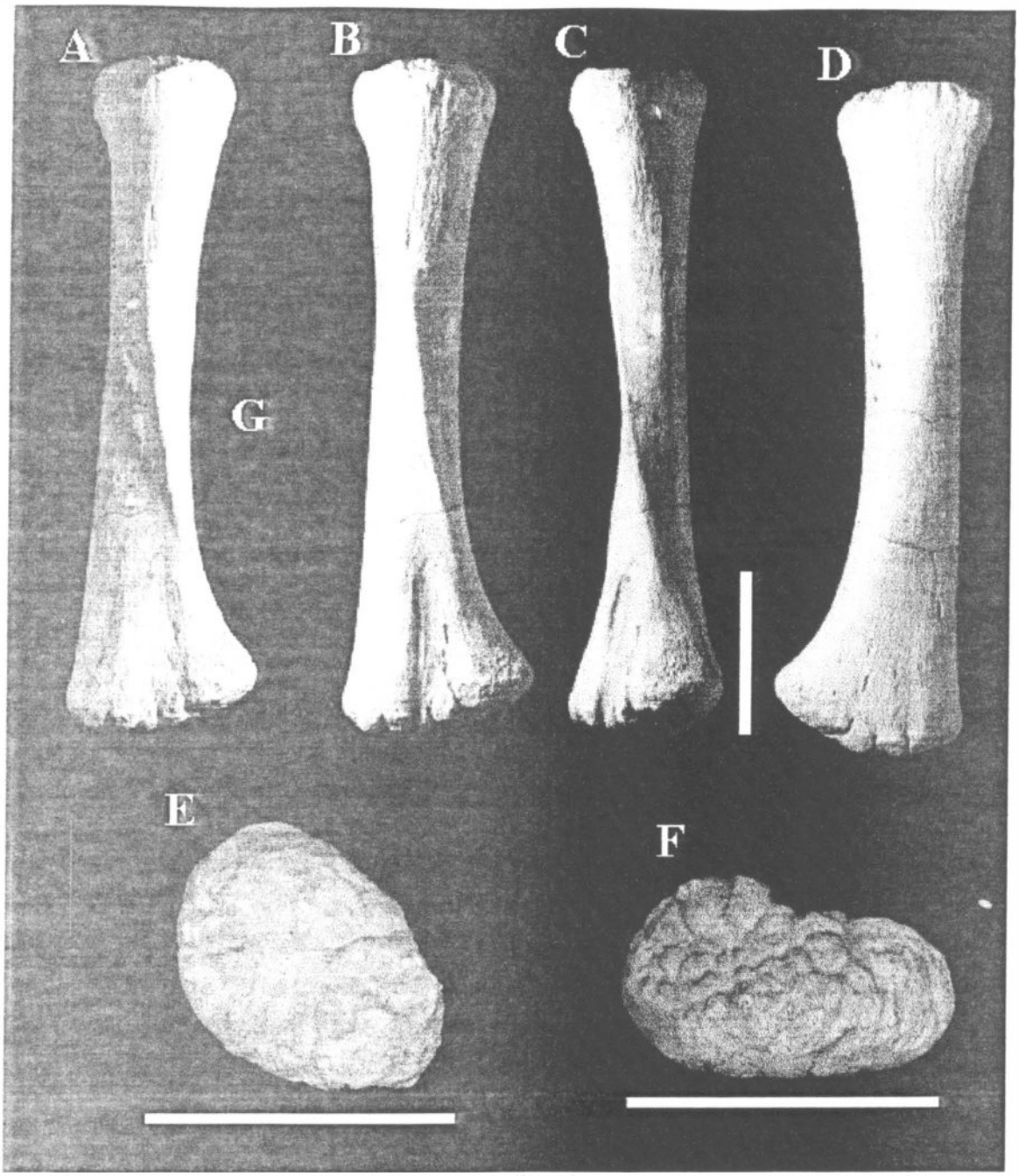


Fig. 76. Right radius MCT 1637-R in: A) posterior (light from the right); B) posterior (light from the left); C) lateral; D) anterior; E) proximal; F) distal views. Scale bar = 10 cm.

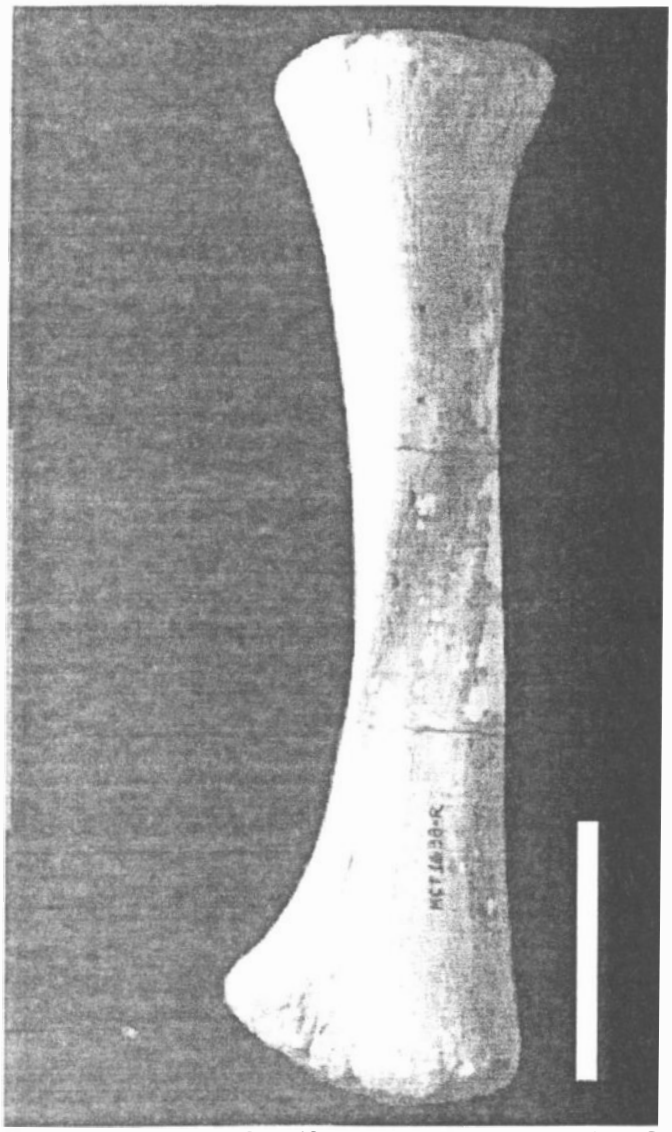


Fig. 77. Left radius MCT 1638-R in posterior (ulnar) view. Scale bar = 10 cm.

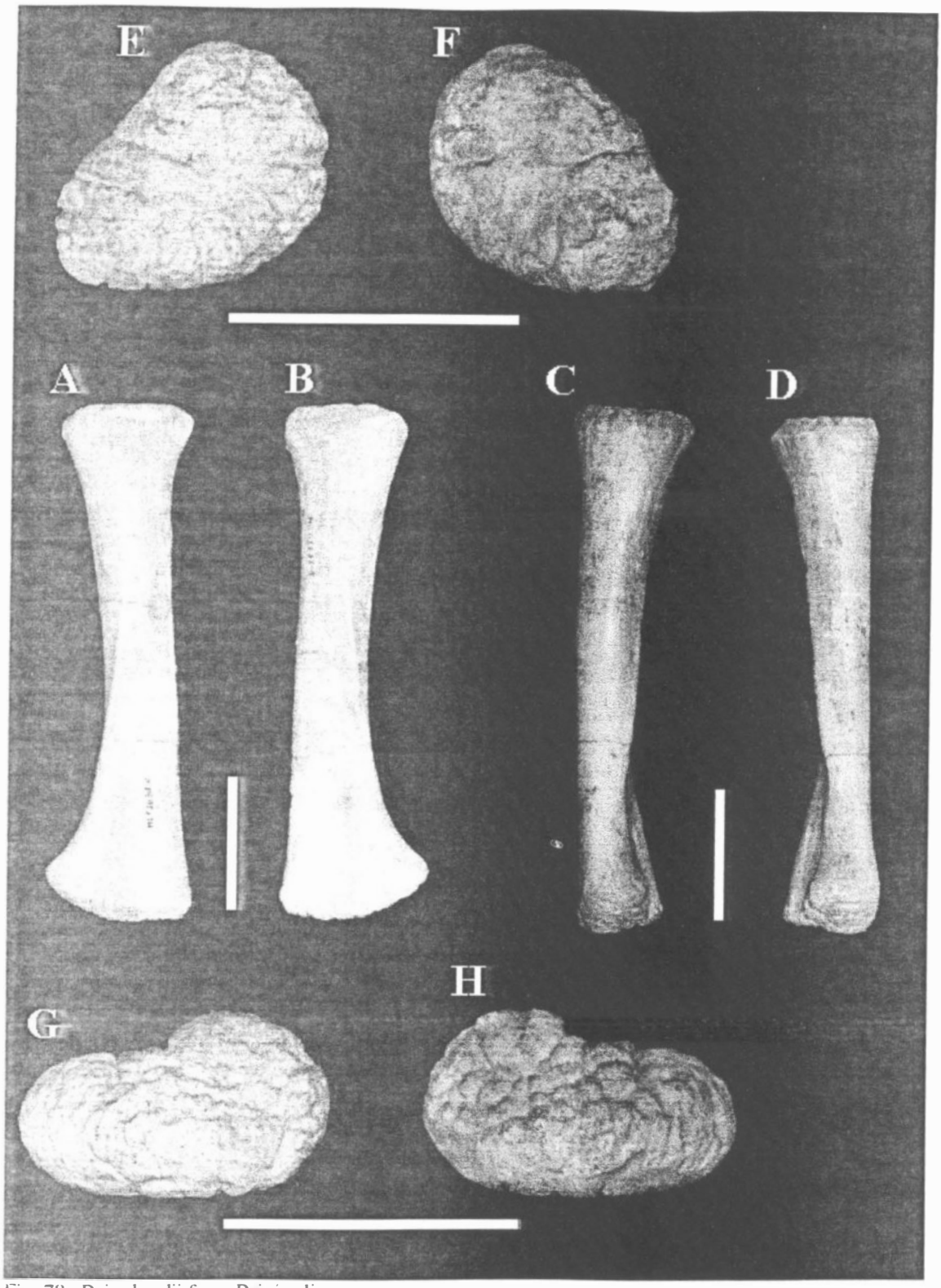


Fig. 78. Paired radii from Peirópolis.
Left radius MCT 1638-R in: A) posterior; C) lateral; E) proximal and G) distal views.
Right radius MCT 1637-R in: B) posterior; D) lateral; F) proximal and H) distal views.
A and B; C and D; E and F; G and H at same scale. Scale bar = 10 cm.

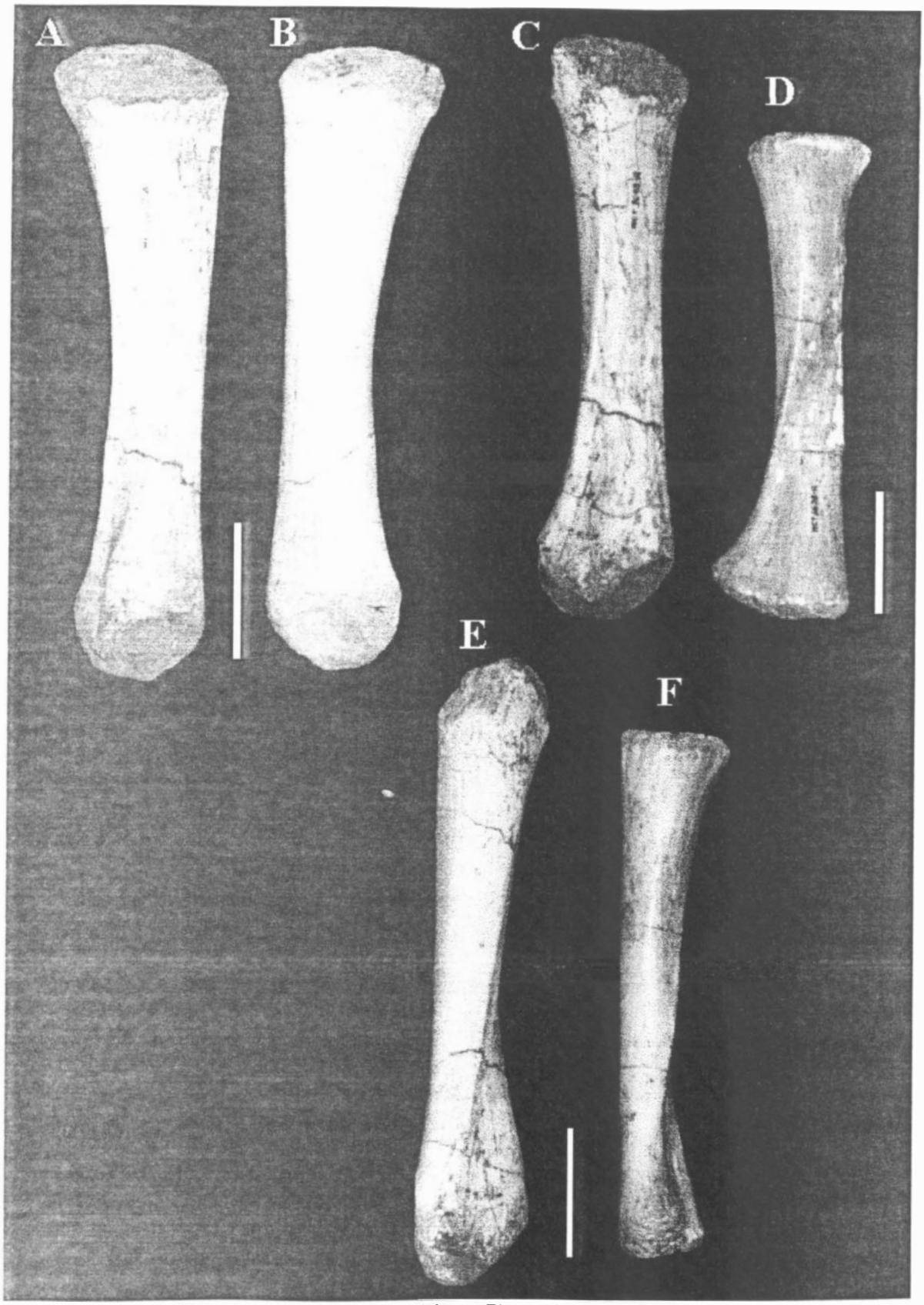


Fig. 79. Left radius MCT 1648-R in: A) posterior (ulnar); B) anterior; C) posterior and E) lateral views. Left radius MCT 1638-R in: D) posterior and F) lateral views, for comparison. A and B; C and D; E and F at same scale. Scale bar = 10 cm.

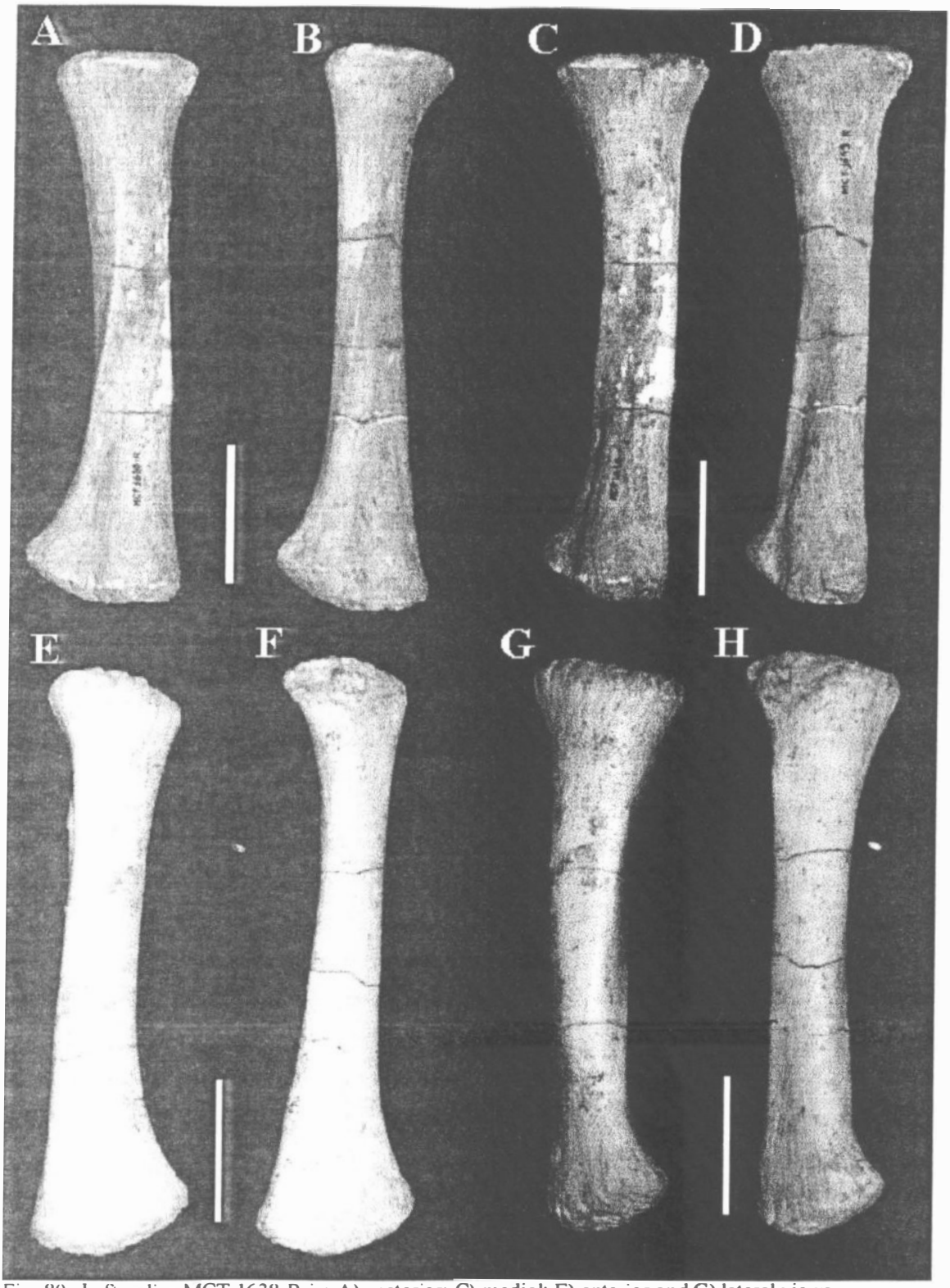


Fig. 80. Left radius MCT 1638-R in: A) posterior; C) medial; E) anterior and G) lateral views. Left radius MCT 1649-R in: B) posterior; D) medial; F) anterior and H) lateral views. For comparison. A and B; C and D; E and F; G and H at same scale. Scale bar = 10 cm.

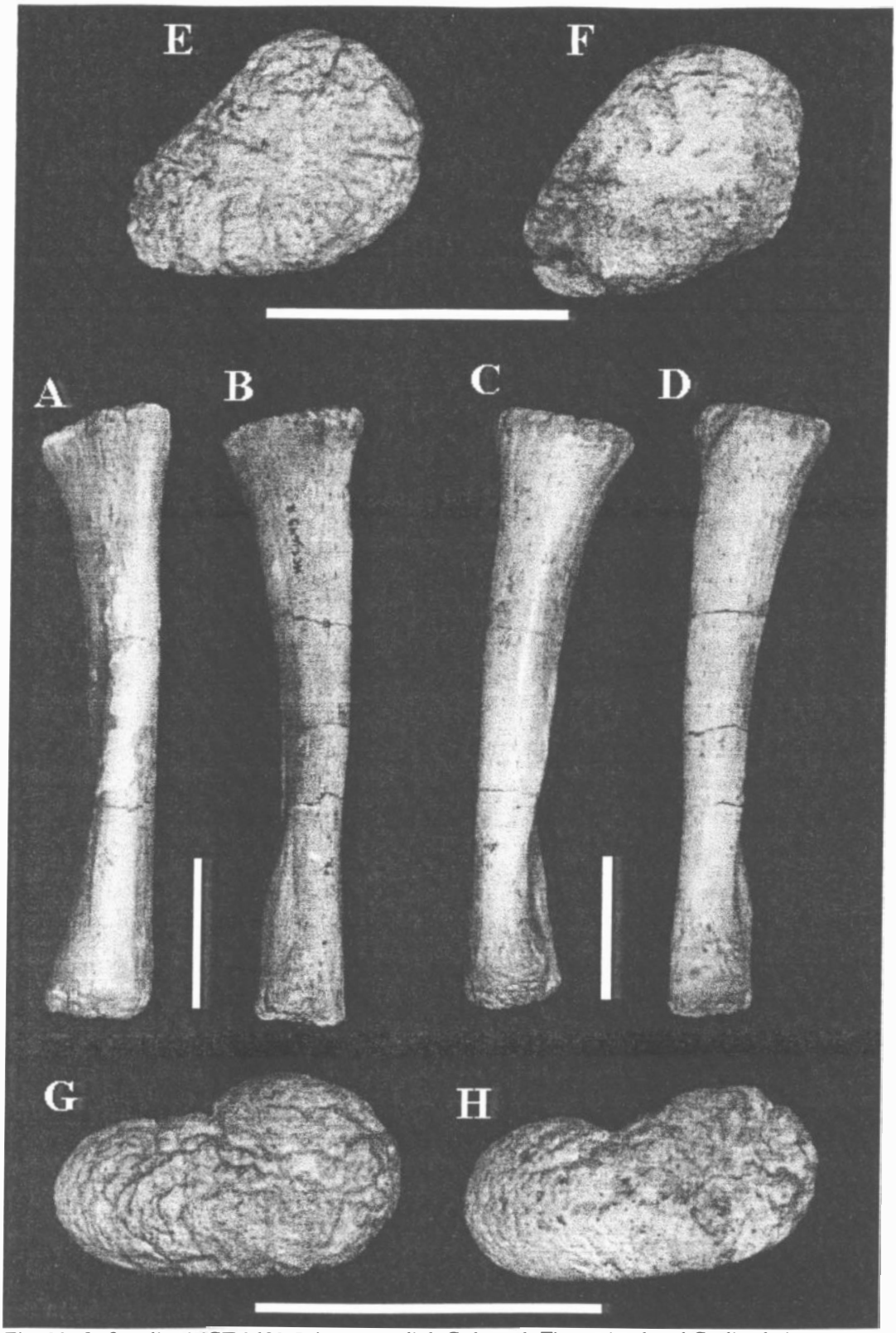


Fig. 81. Left radius MCT 1638-R in: A) medial; C) lateral; E) proximal and G) distal views. Left radius MCT 1649-R in: B) medial; D) lateral; F) proximal and H) distal views. For comparison. A and B; C and D; E and F; G and H at same scale. Scale bar = 10 cm.

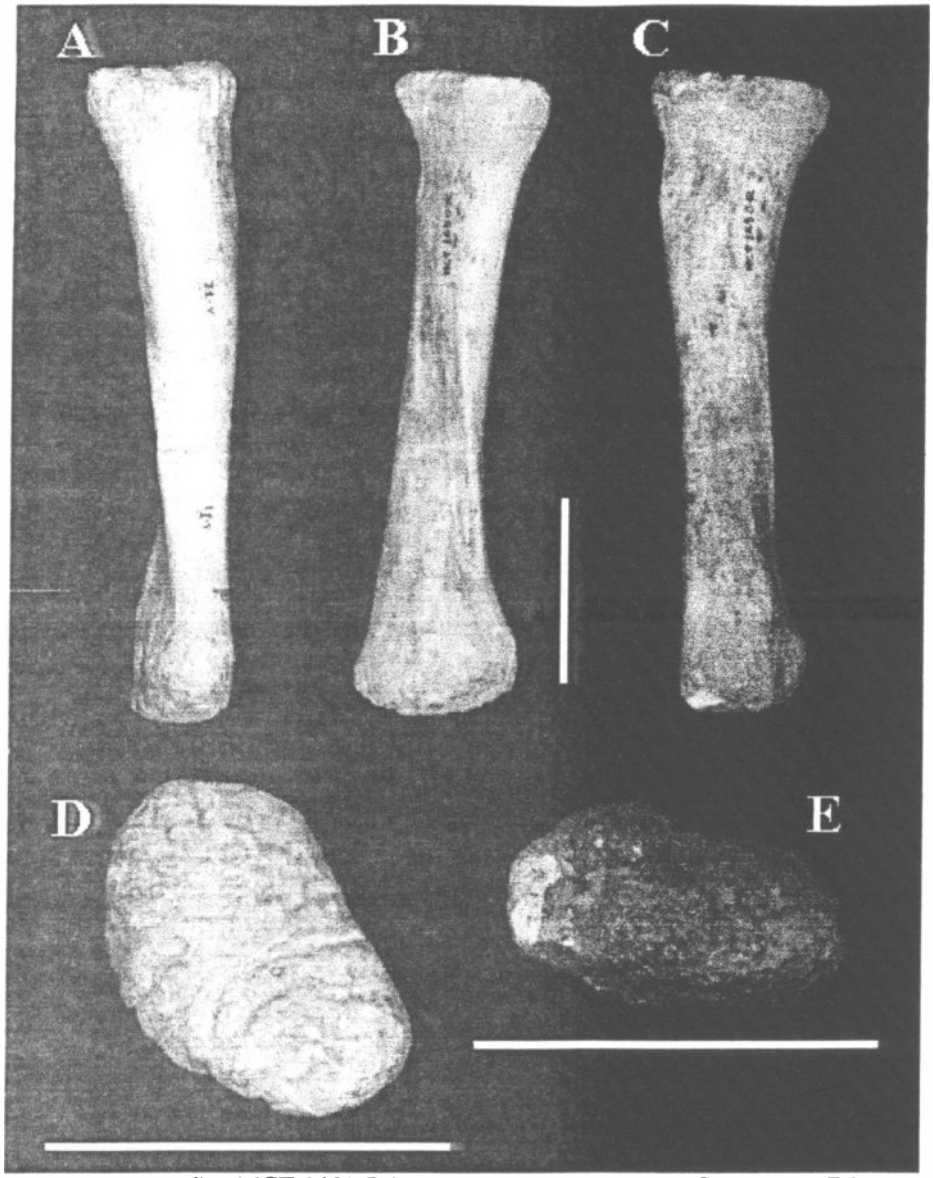


Fig. 82. Right radius MCT 1650-R in: A) lateral; B) posterior; C) anterior; D0 proximal and E) distal views. Scale bar = 10 cm.

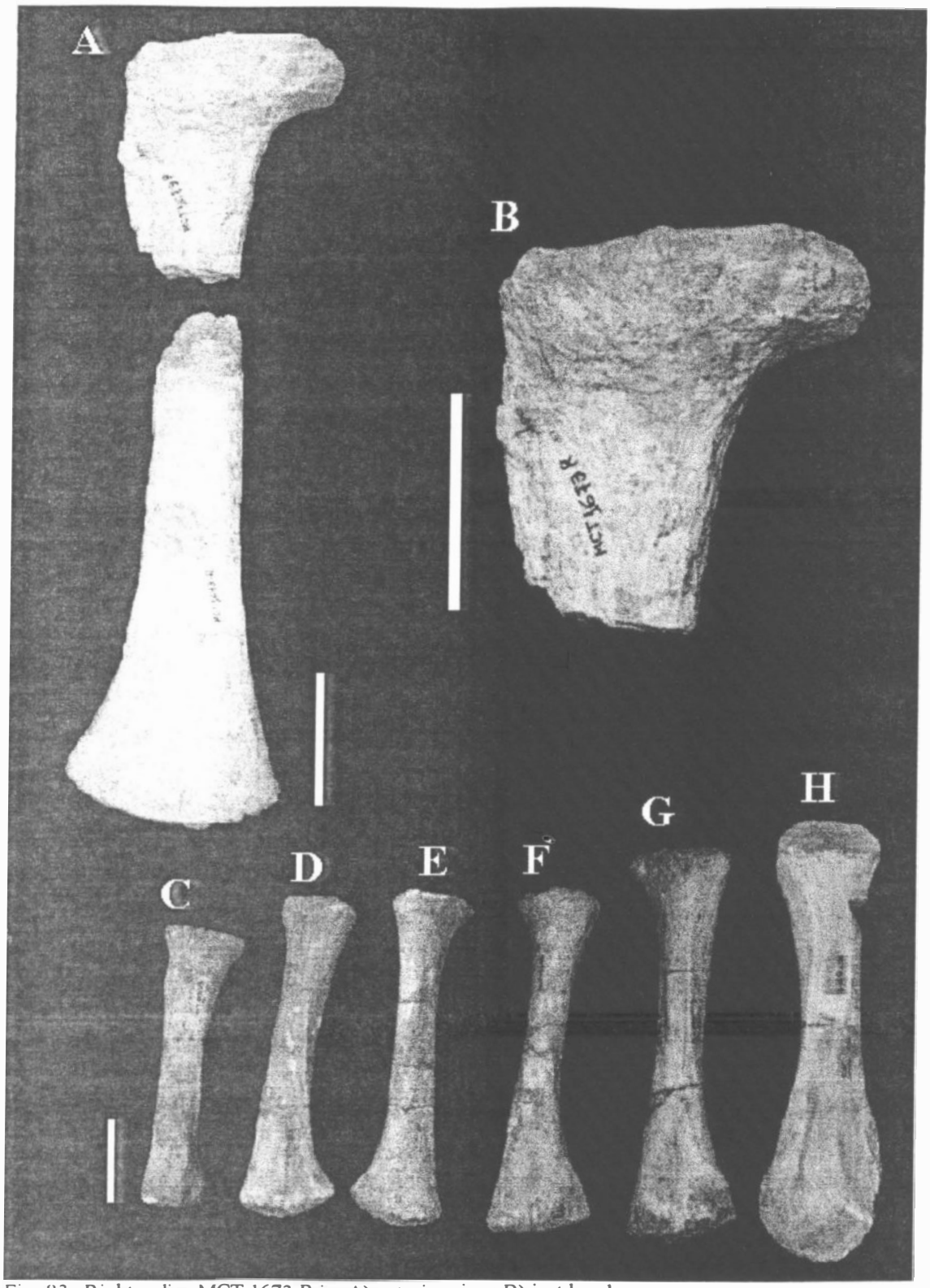


Fig. 83. Right radius MCT 1673-R in: A) anterior view; B) just head.
C to H: Radii from Peirópolis, for size comparison: C) MCT 1650-R; D) MCT 1637-R; E) MCT 1649-R; F) MCT 1610-R; G) MCT 1636-R; H) MCT 1595-R. All to same scale. Scale bar = 10 cm.

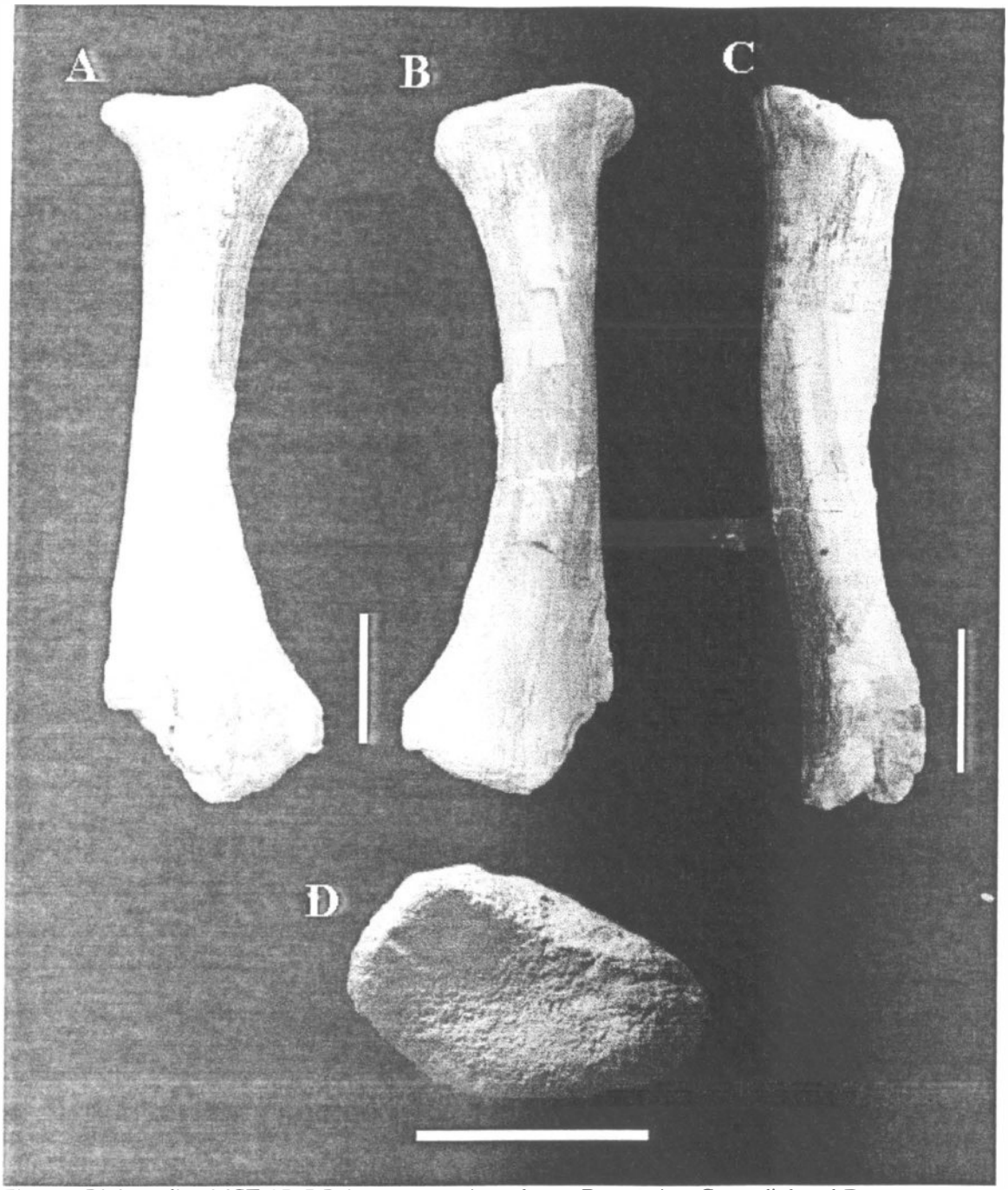


Fig. 84. Right radius MCT 1707-R in: A) posterior (ulnar); B) anterior; C) medial and D) proximal views. Scale bar = 10 cm.

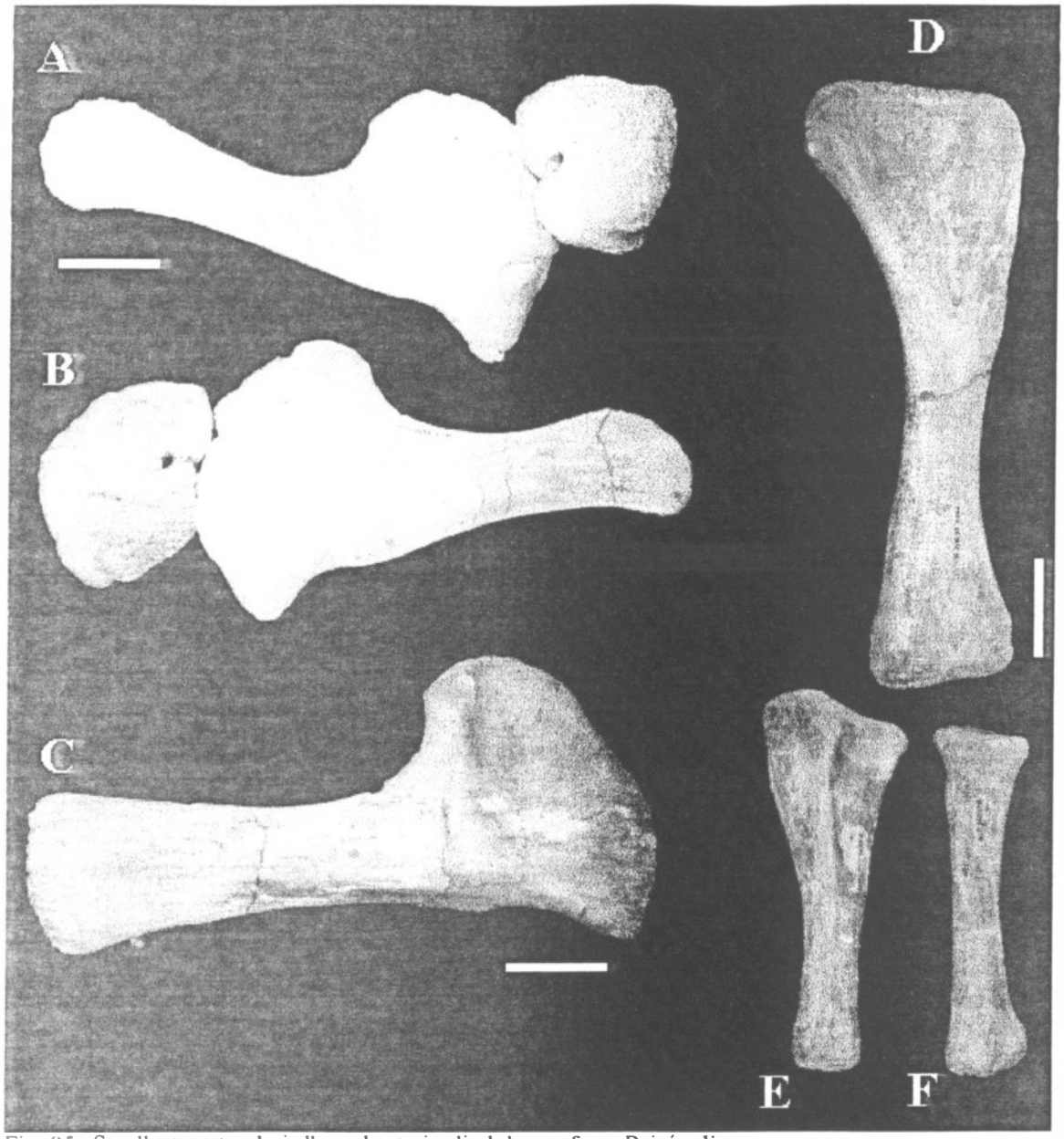


Fig. 85. Smallest pectoral girdle and anterior limb bones from Peirópolis:
Left scapula MCT 1652-R and left coracoid MCT 1653-R in: A) medial and B) lateral views
C) Right scapula MCT 1680-R in lateral view, for size comparison
D to F) Smallest anterior limb bones from Peirópolis: D) Left humerus MCT 1674-R, E) Right ulna MCT 1651-R and F) Right radius MCT 1650-R
All at the same scale. Scale bar = 10 cm.

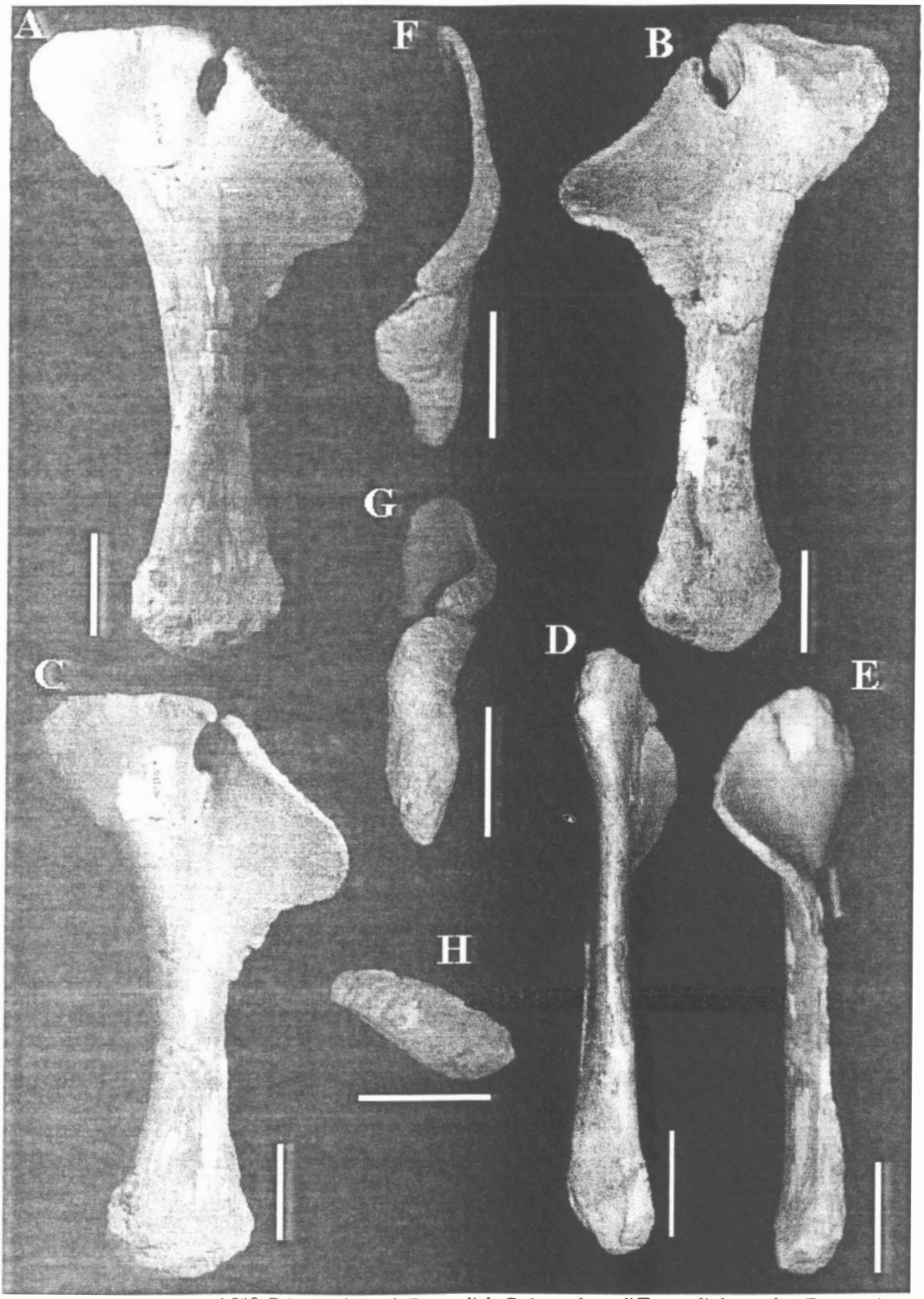


Fig. 86. Left pubis MCT 1592-R in: A) lateral; B) medial; C) lateral (at different light angle); D) anterior; E) posterior; F) proximal (ischial); G) proximal (iliac) and H) distal views. Scale bar = 10 cm.

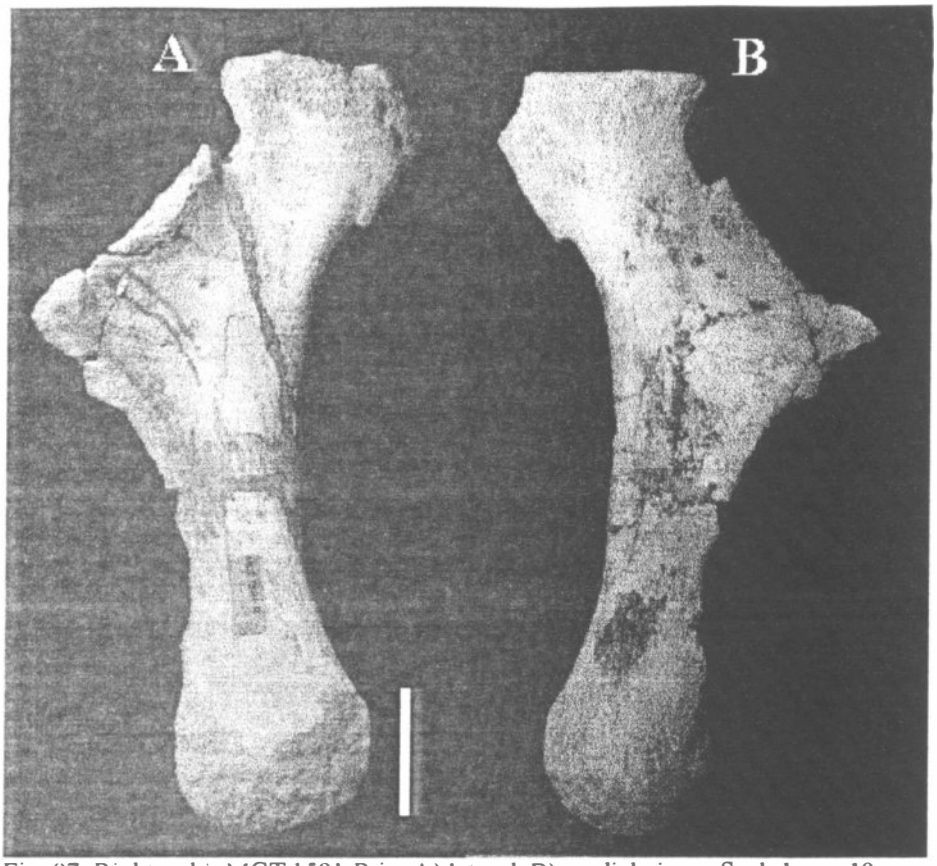


Fig. 87. Right pubis MCT 1591-R in: A) lateral; B) medial views. Scale bar = 10 cm.

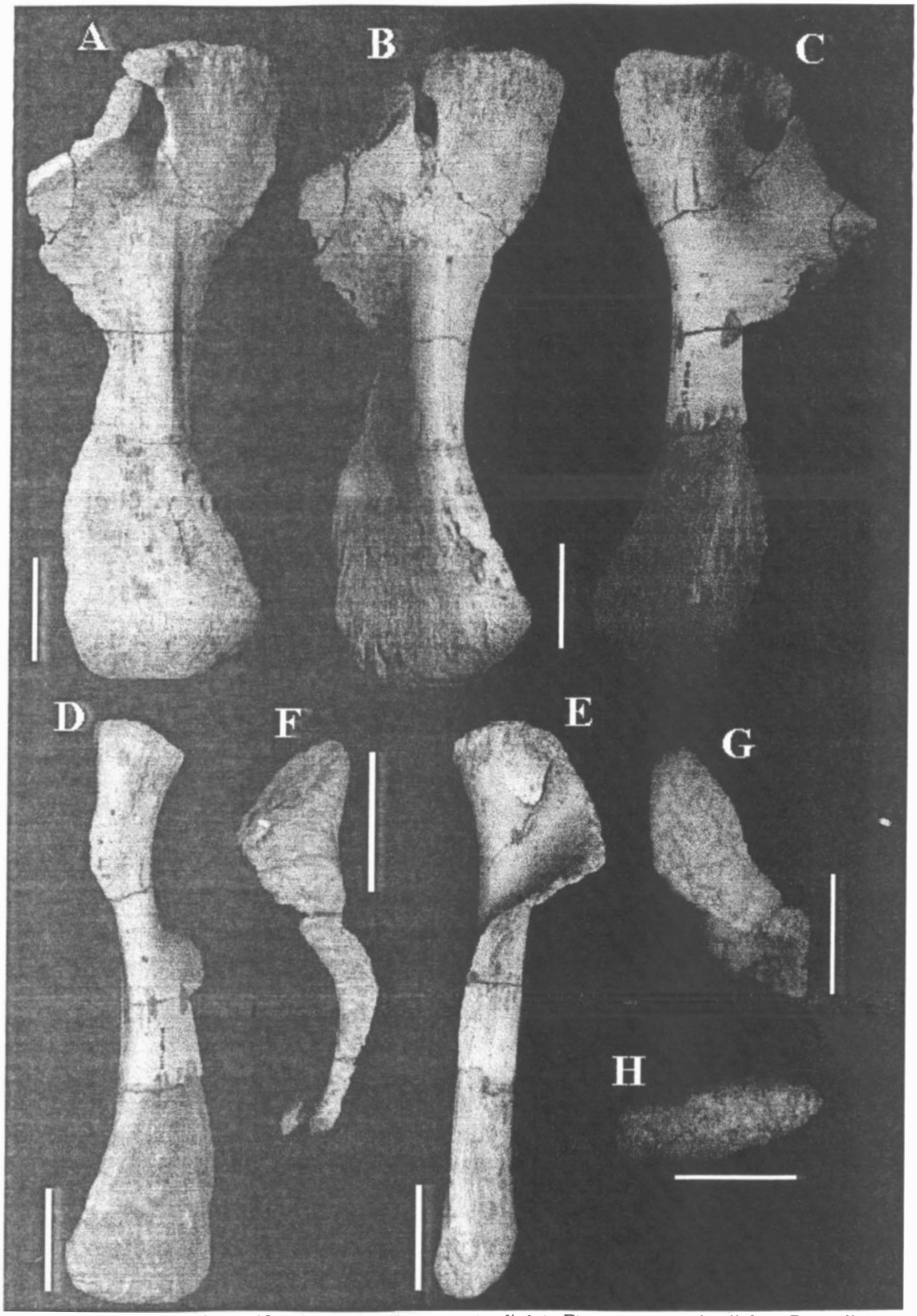


Fig. 88. Right pubis MCT 1640-R in: A) lateral (posterior light); B) lateral (anterior light); C) medial; D) anterior; E) posterior; F) proximal (ischial); G) proximal (iliac) and H) distal views. Scale bar = 10 cm.

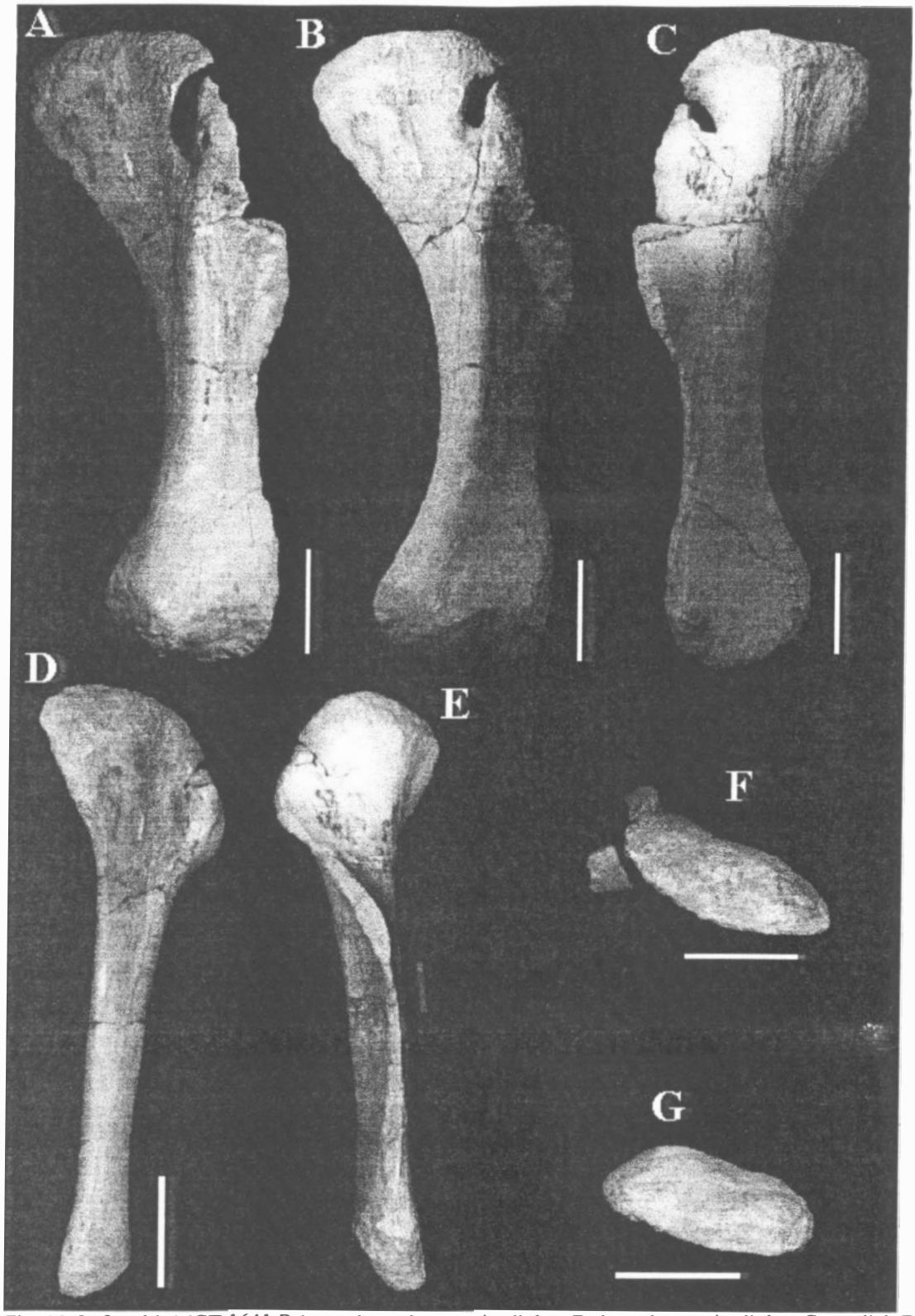


Fig. 89. Left pubis MCT 1641-R in: A) lateral (posterior light); B) lateral (anterior light); C) medial; D) anterior; E) posterior; F) proximal (iliac) and G) distal views. Scale bar = 10 cm.

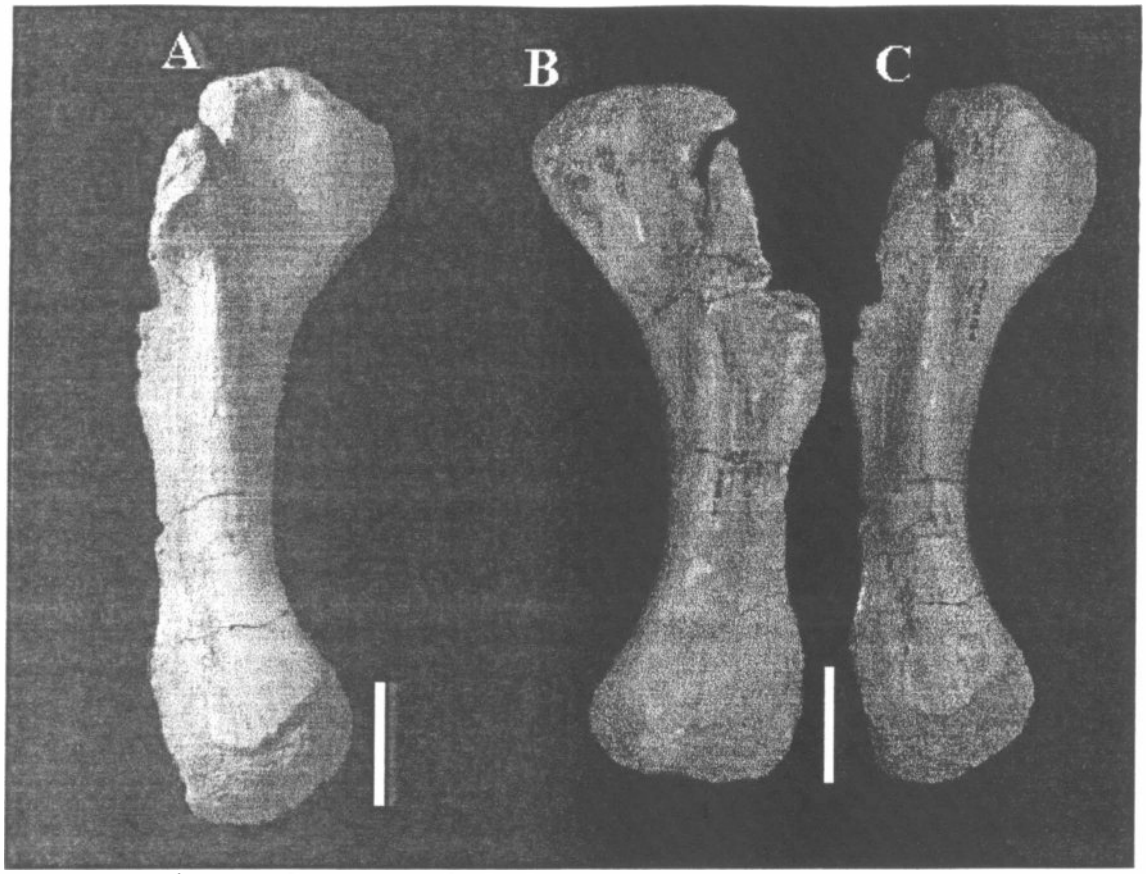


Fig. 90. A) Right pubis MCT 1675-R in lateral view.
Pair of pubes in lateral view: B) Left pubis MCT 1641-R and C) Right pubis MCT 1675-R. Scale bar = 10 cm.

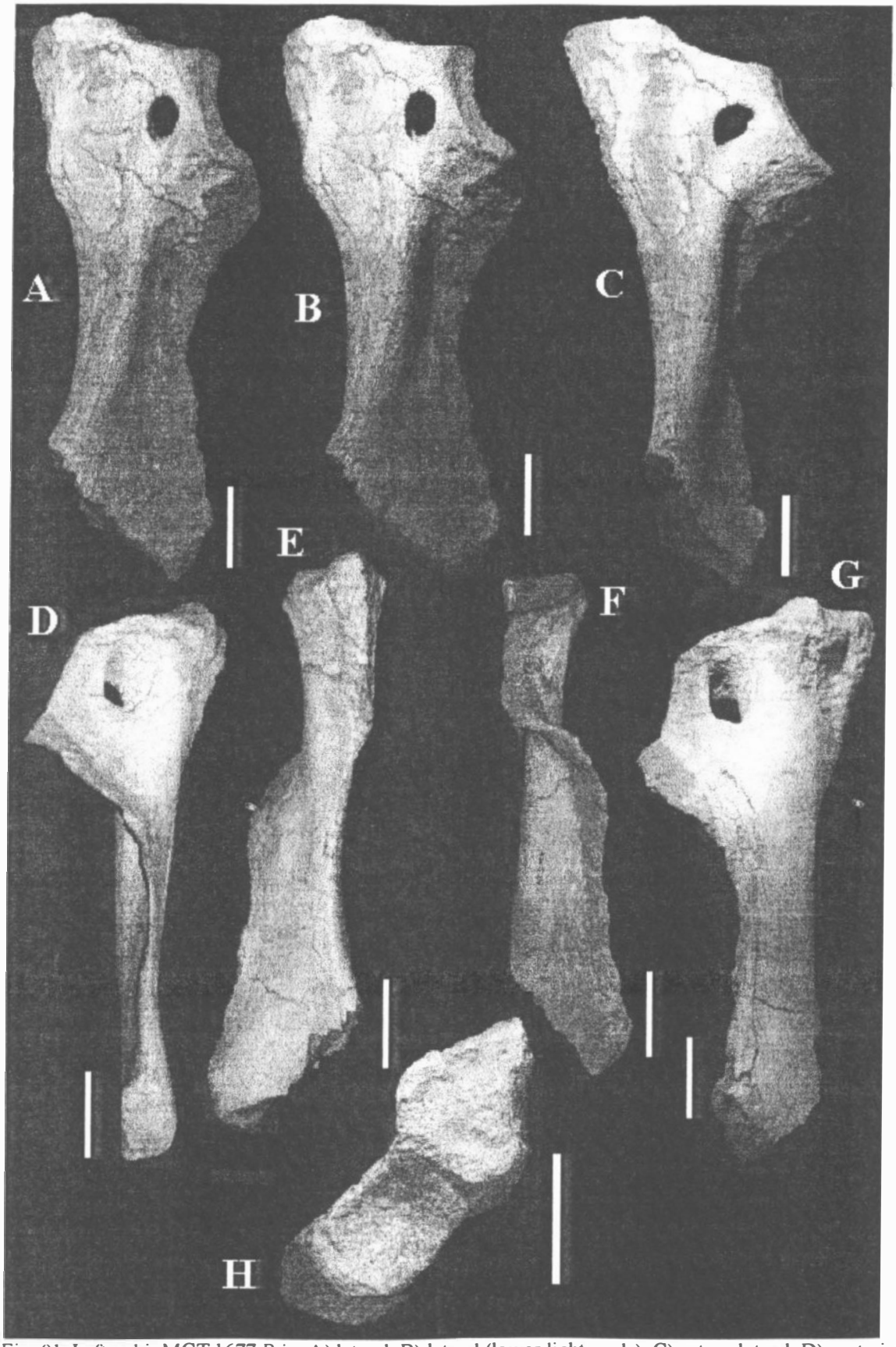


Fig. 91. Left pubis MCT 1677-R in: A) lateral; B) lateral (lower light angle); C) antero-lateral; D) posterior; E) anterior; F) posterior (showing pubic symphysis), G)medio-posterior and H) proximal (iliac) views. Scale bar = 10 cm.

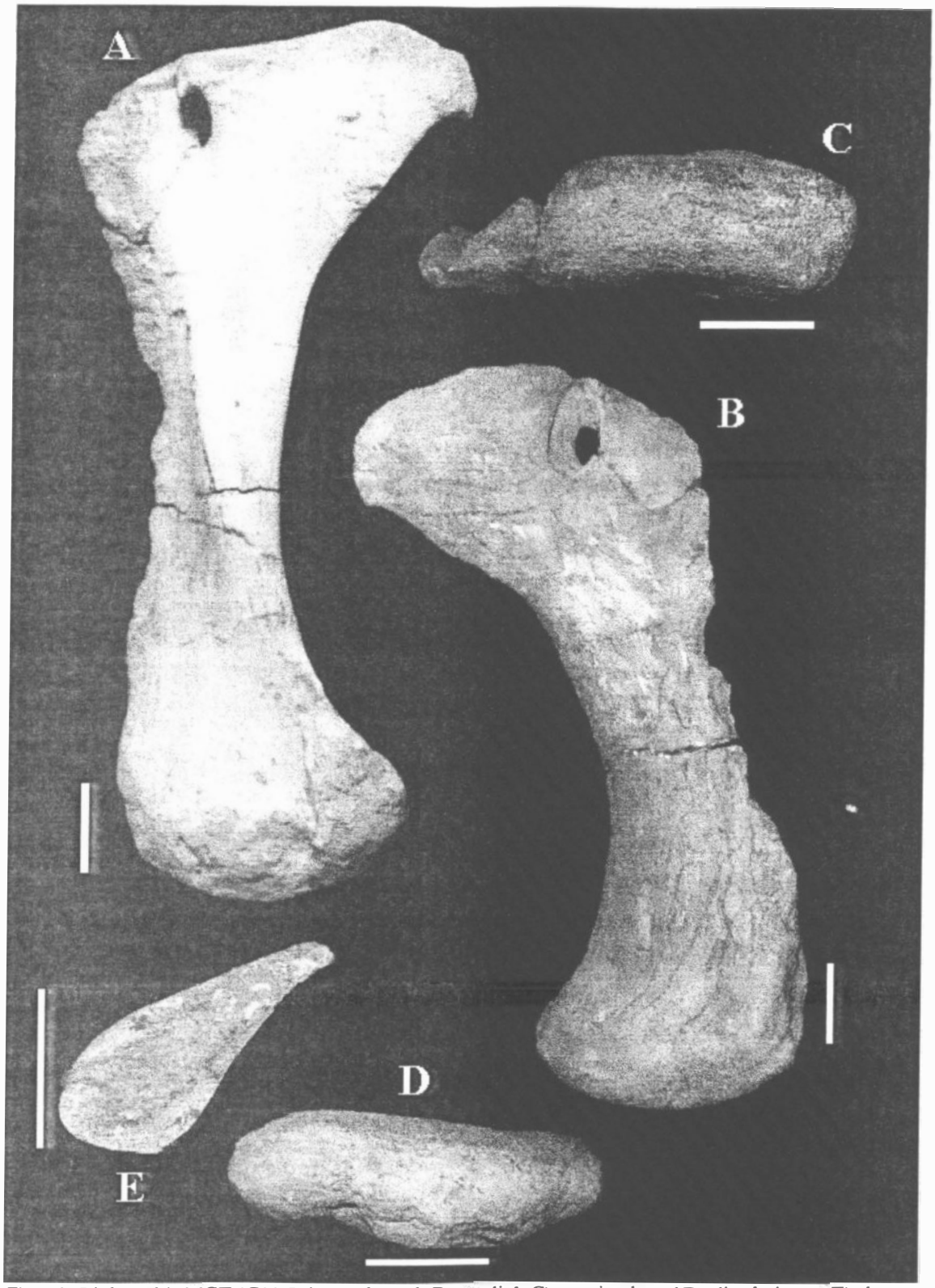


Fig. 92. Right pubis MCT 1711-R in: A) lateral; B) medial; C) proximal; and D) distal views. E) shows a cross-section of the shaft. Scale bar = 10 cm.

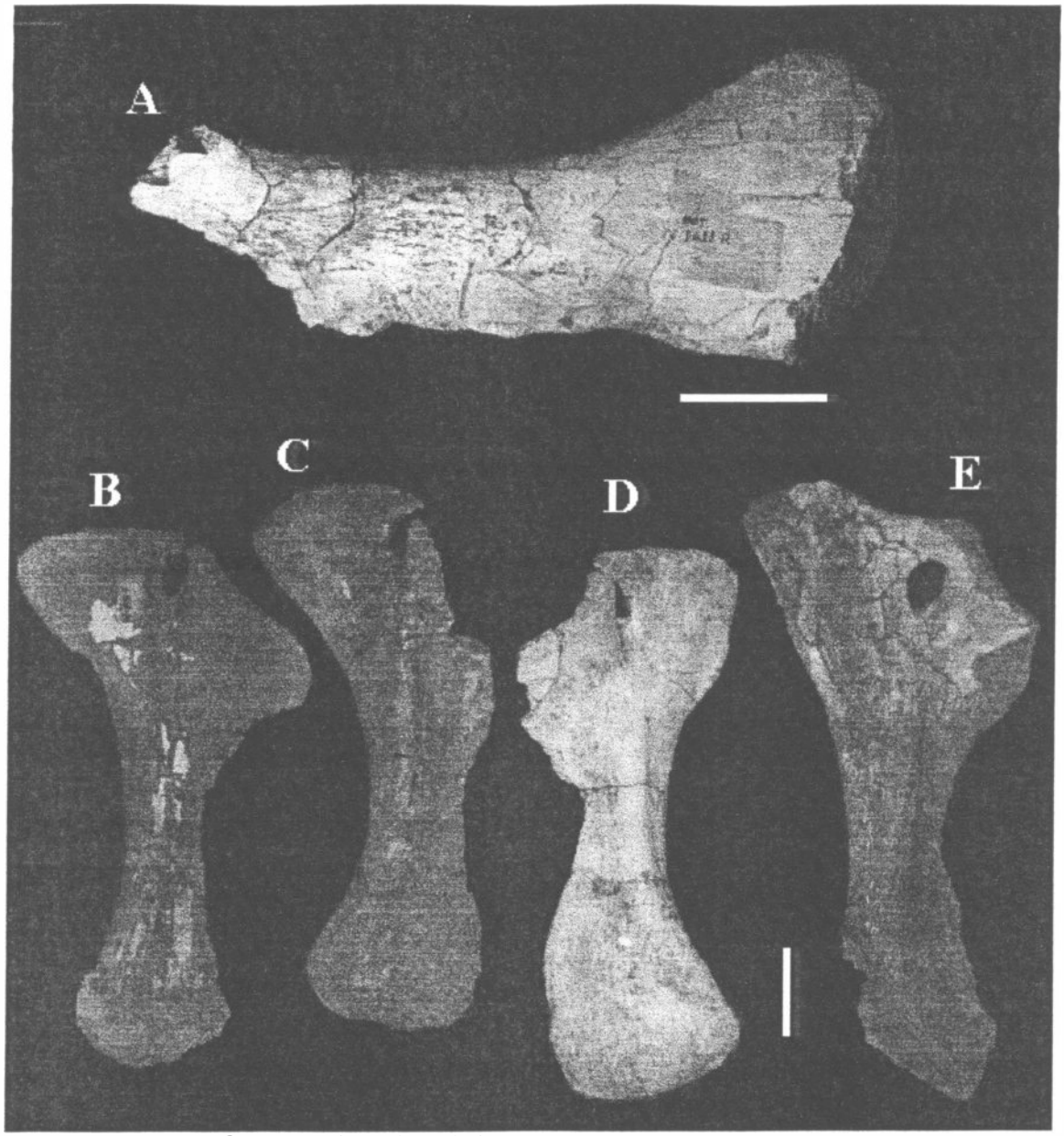


Fig. 93. Left pubis MCT 1611-R in A) lateral view.
Pubes from Peirópolis, for size comparison: B) MCT 1592-R; C) MCT 1641-R; D) MCT 1640-R and E) MCT 1677-R. All lateral views, and at same scale. Scale bar = 10 cm.

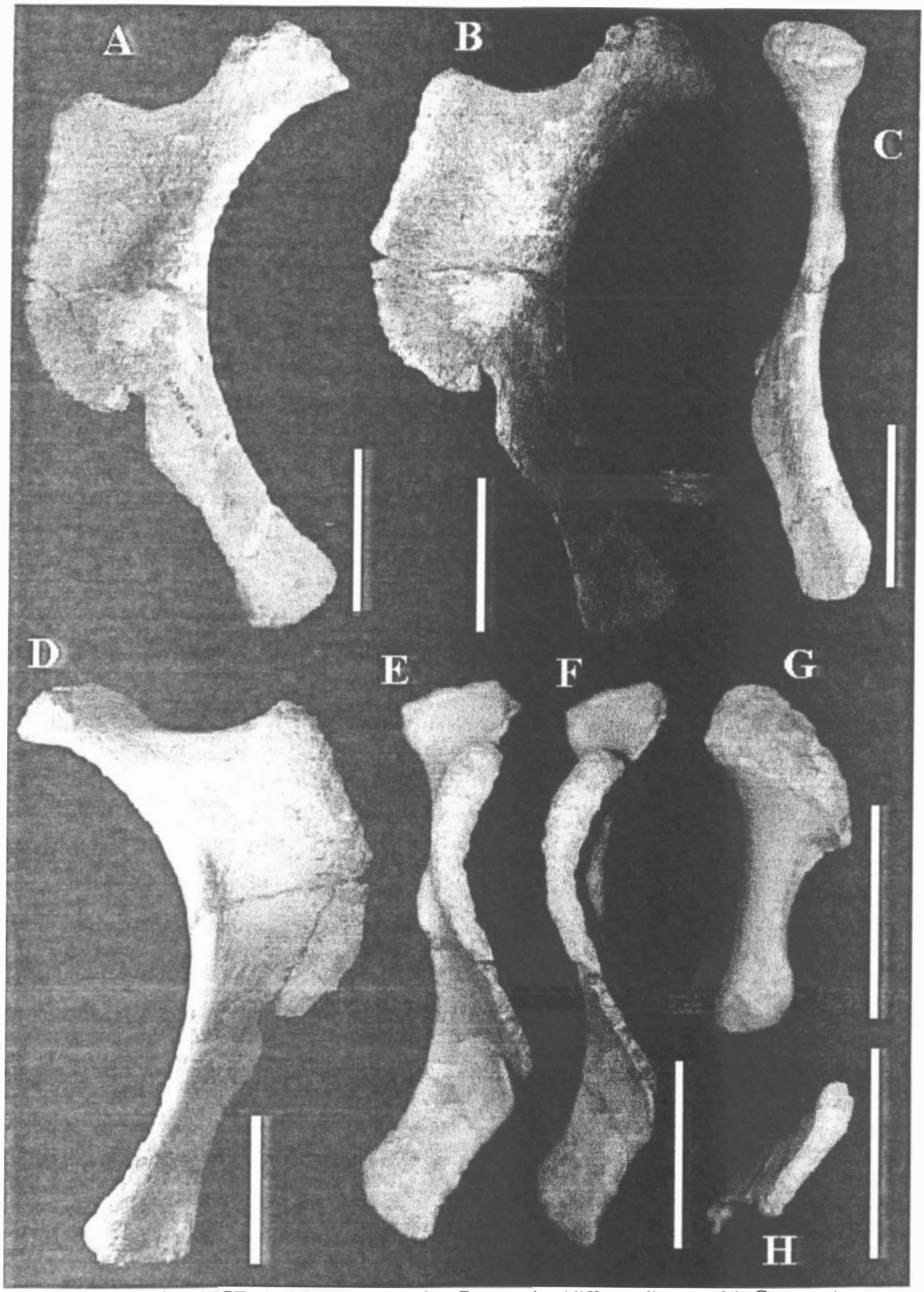


Fig. 94. Right ischium MCT 1586-R in: A) superior; B) superior (different light angle); C) posterior, D) inferior; E) anterior (pubic); F) anterior (slightly different angle); G) proximal (iliac) and H) distal views. Scale bar = 10 cm.

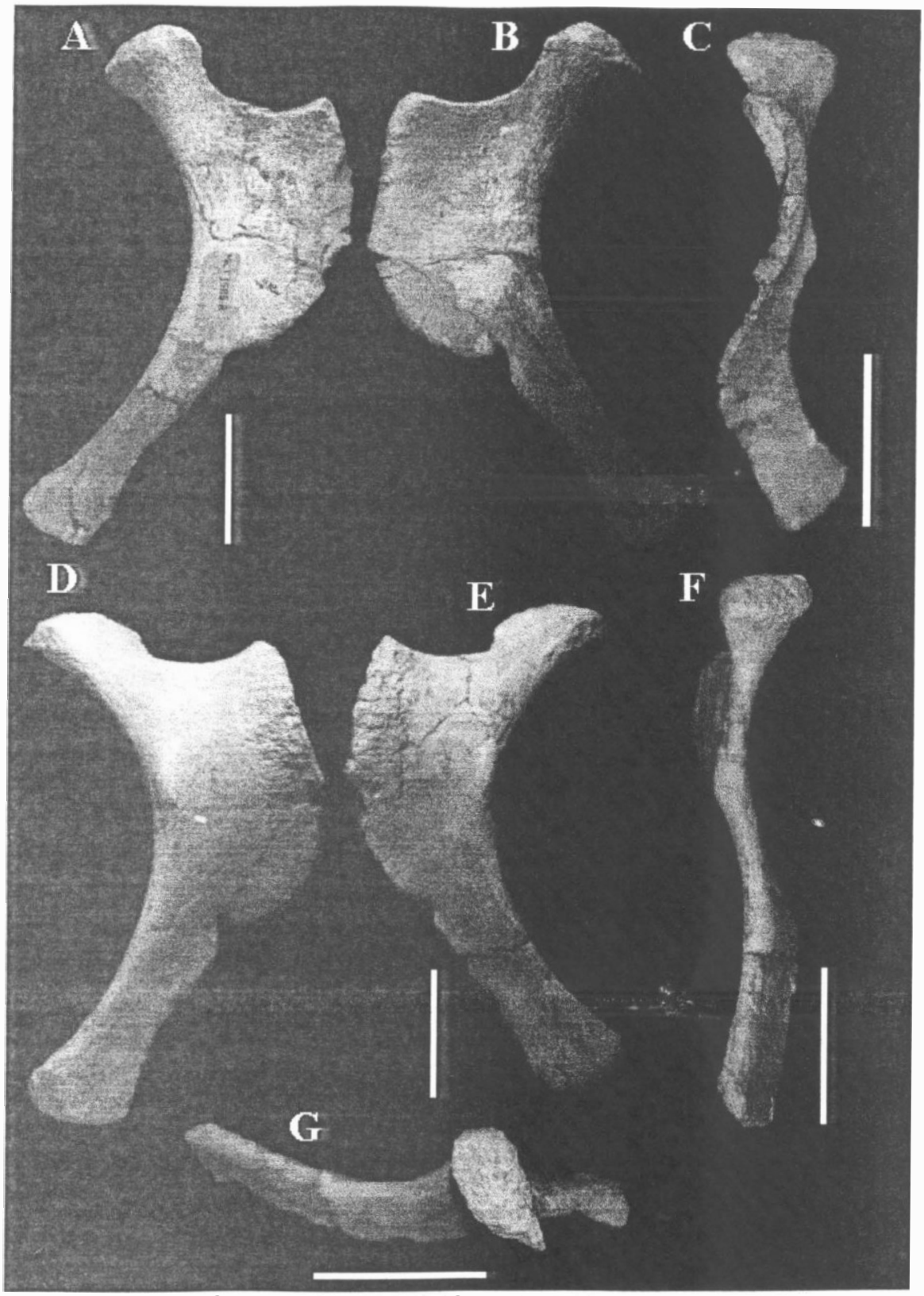


Fig. 95. Left ischium MCT 1585-R in: A) superior; C) anterior (pubic); D) inferior; F) posterior and G) proximal (iliac) views.

Paired right ischium MCT 1586-R in; B) superior and E) posterior views.

A and B; D and E at the same scale. Scale bar = 10 cm.

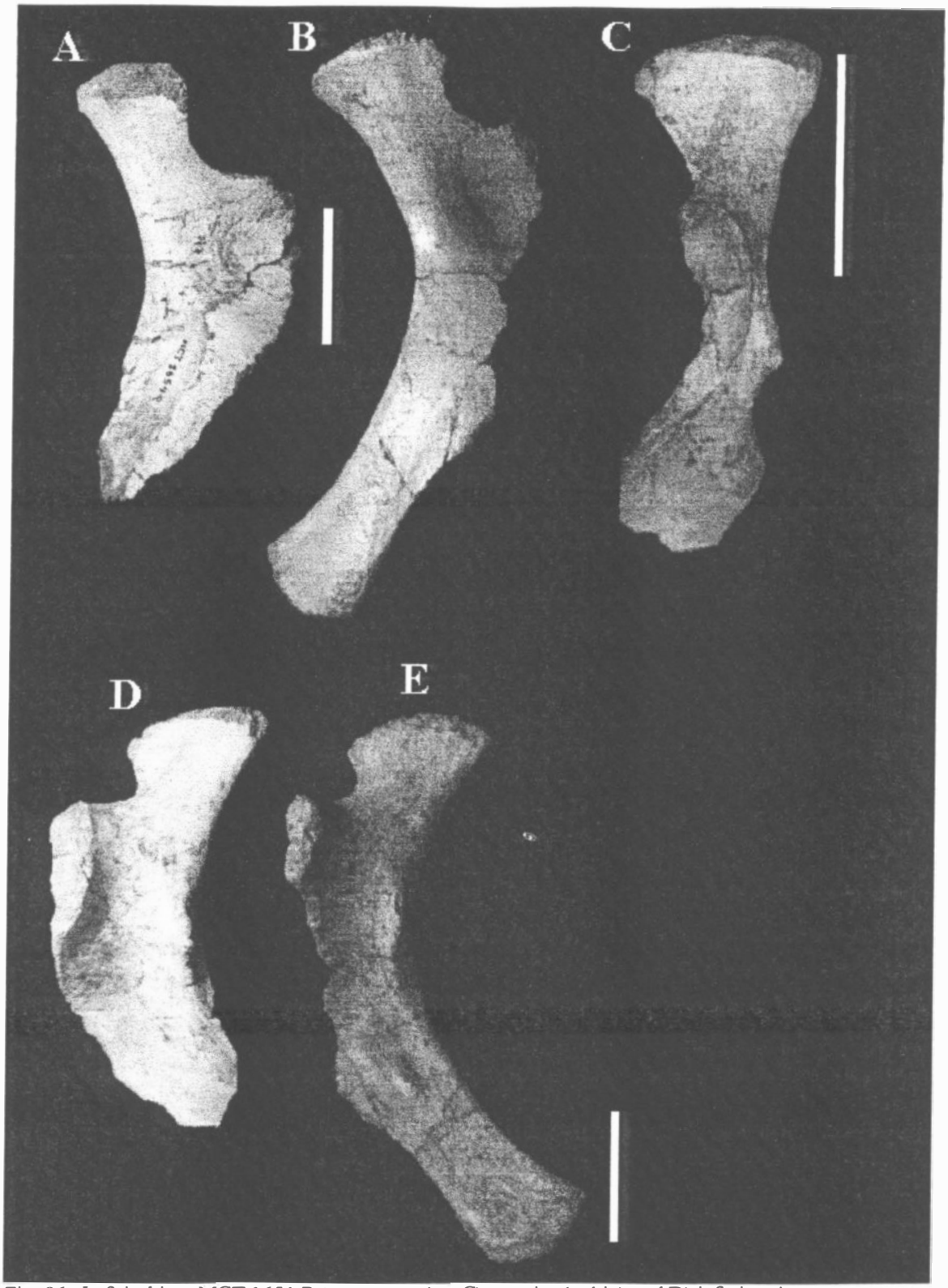


Fig. 96. Left ischium MCT 1654-R in: A) superior; C) anterior (pubic) and D) inferior views. Left ischium MCT 1661-R in: B) superior and E) inferior views, for comparison. A and B; D and E at the same scale. Scale bar = 10 cm.

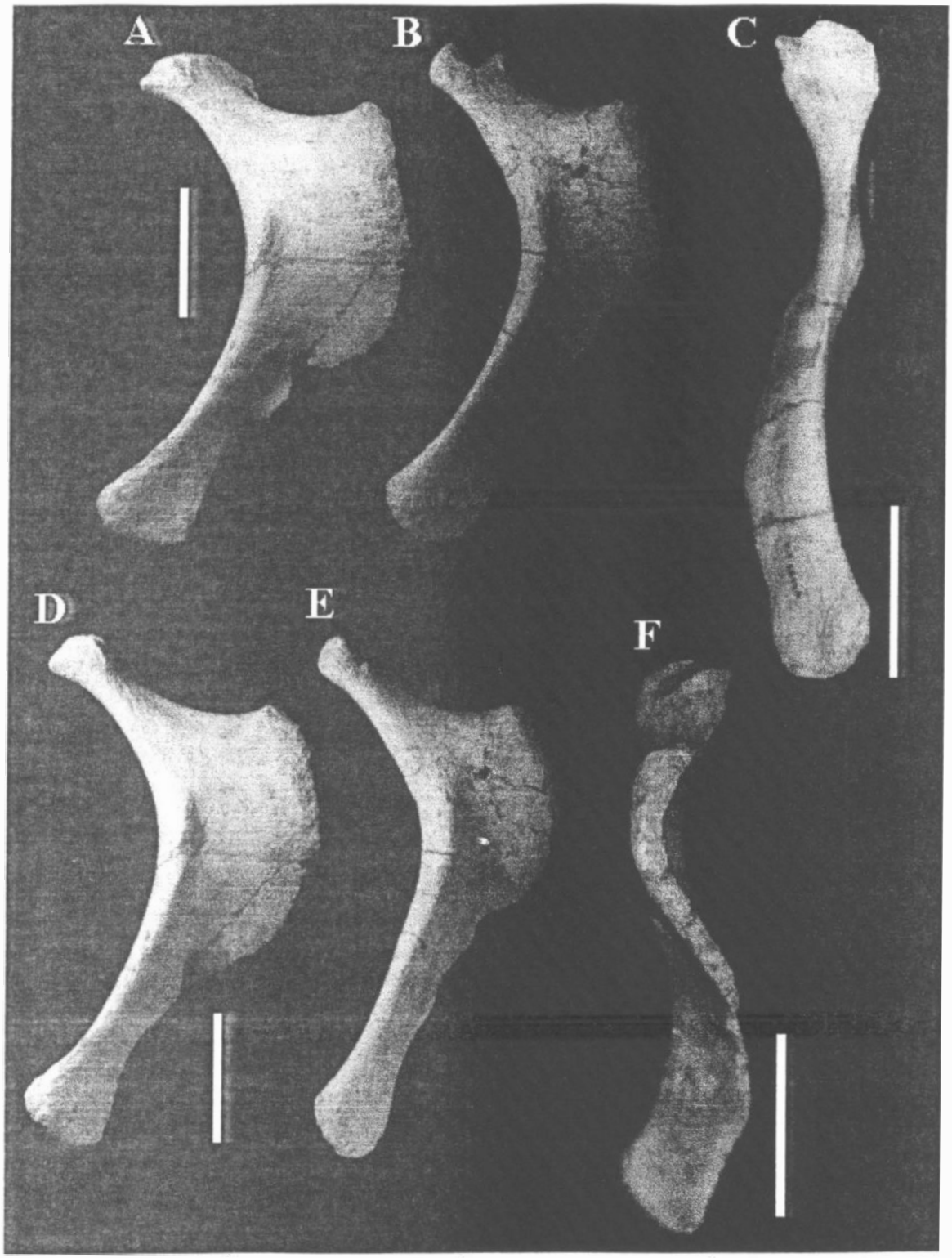


Fig. 97. Right ischium MCT 1655-R in: B) inferior (low light angle); C) posterior; E) inferior and F) anterior (pubic) views.

Right ischium MCT 1586-R in: A) inferior (low light angle) and D) inferior views, for comparison. A and B; D and E to the same scale. Scale bar = 10 cm.

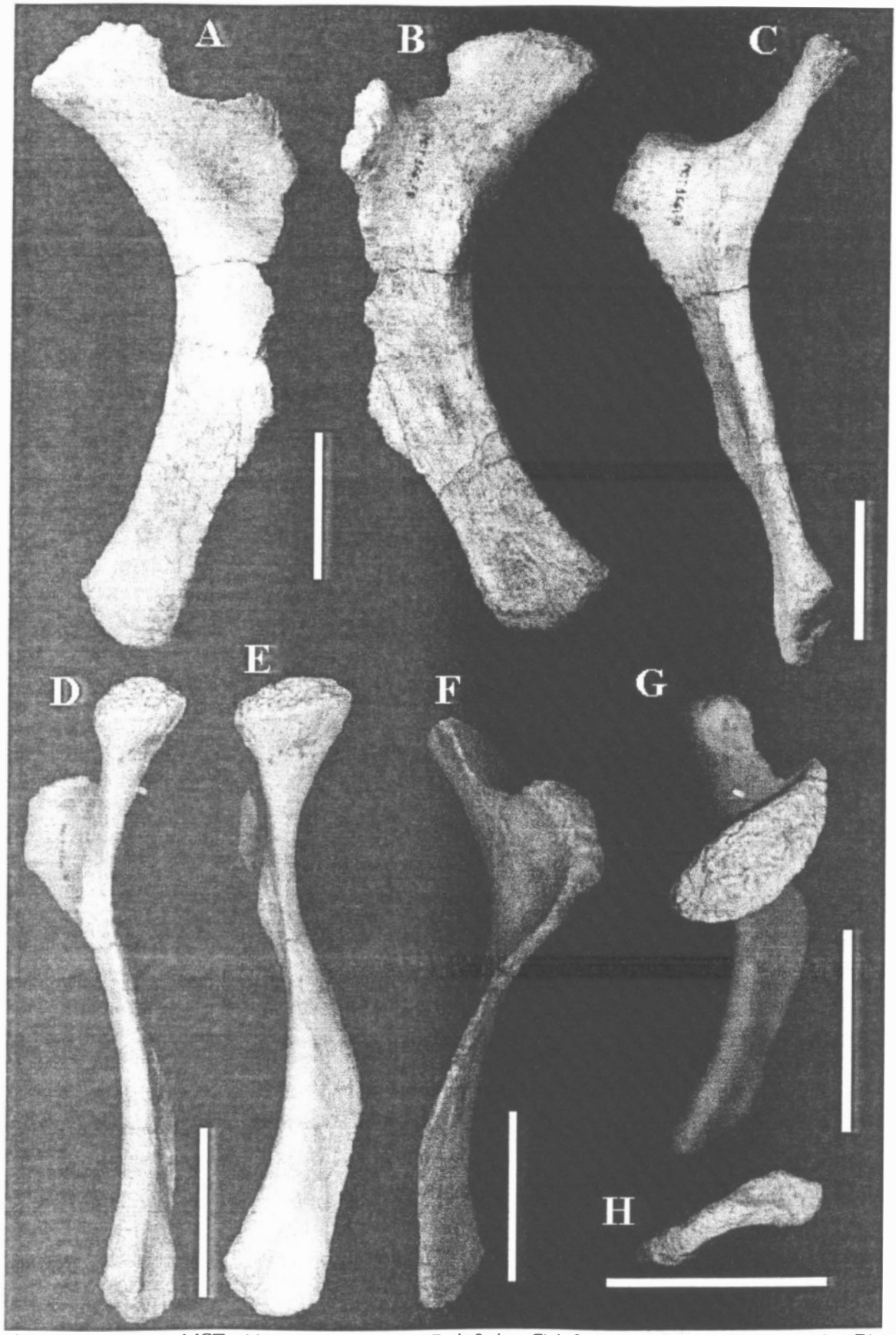


Fig. 98. Left ischium MCT 1661-R in: A) superior; B) inferior; C) inferior (at slightly different angle); D) posterior; E) posterior (at slightly different angle); F) anterior (pubic); G) proximal (iliac) and H) distal views. Scale bar = 10 cm.

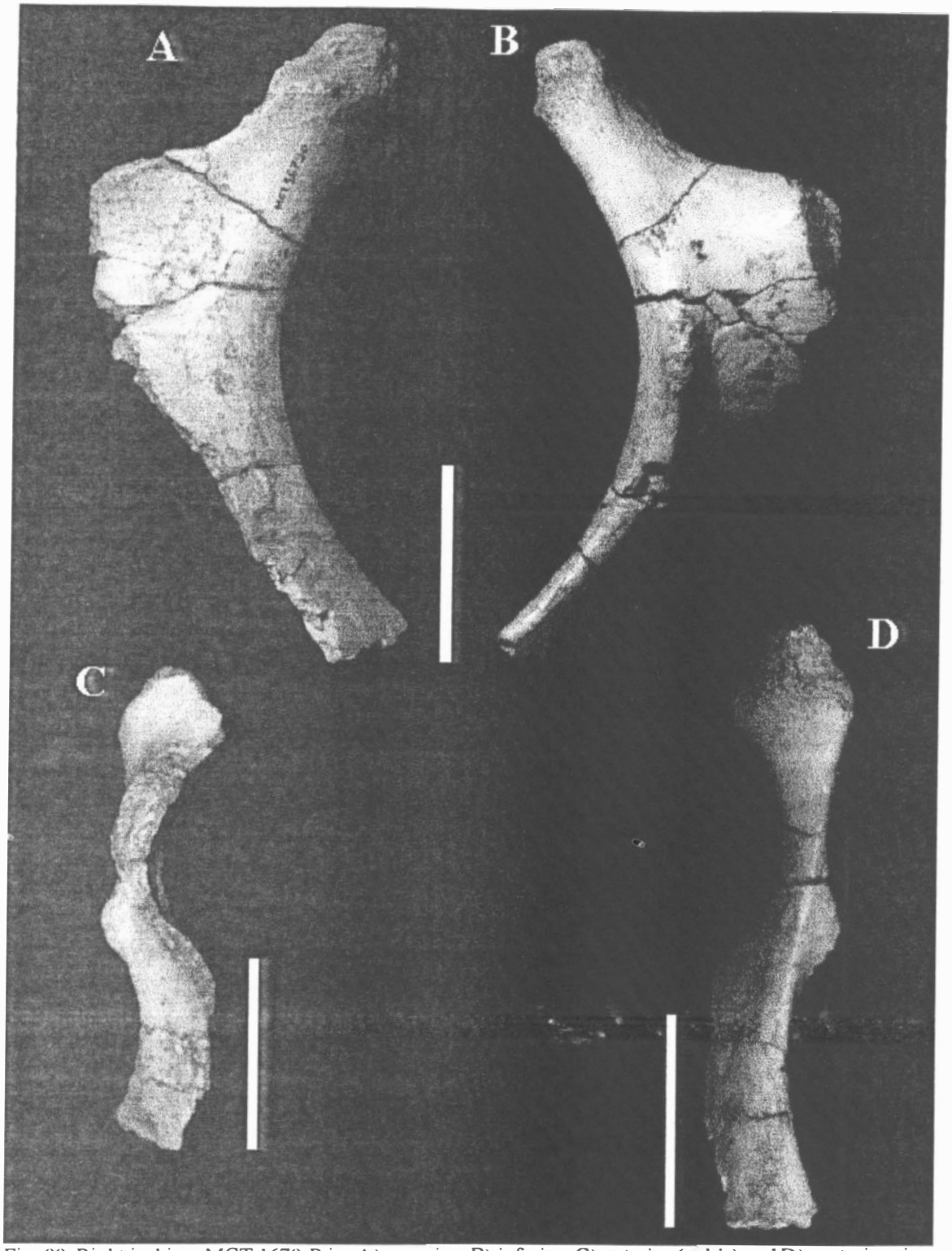


Fig. 99. Right ischium MCT 1679-R in: A) superior; B) inferior; C) anterior (pubic) and D) posterior views. Scale bar = 10 cm.

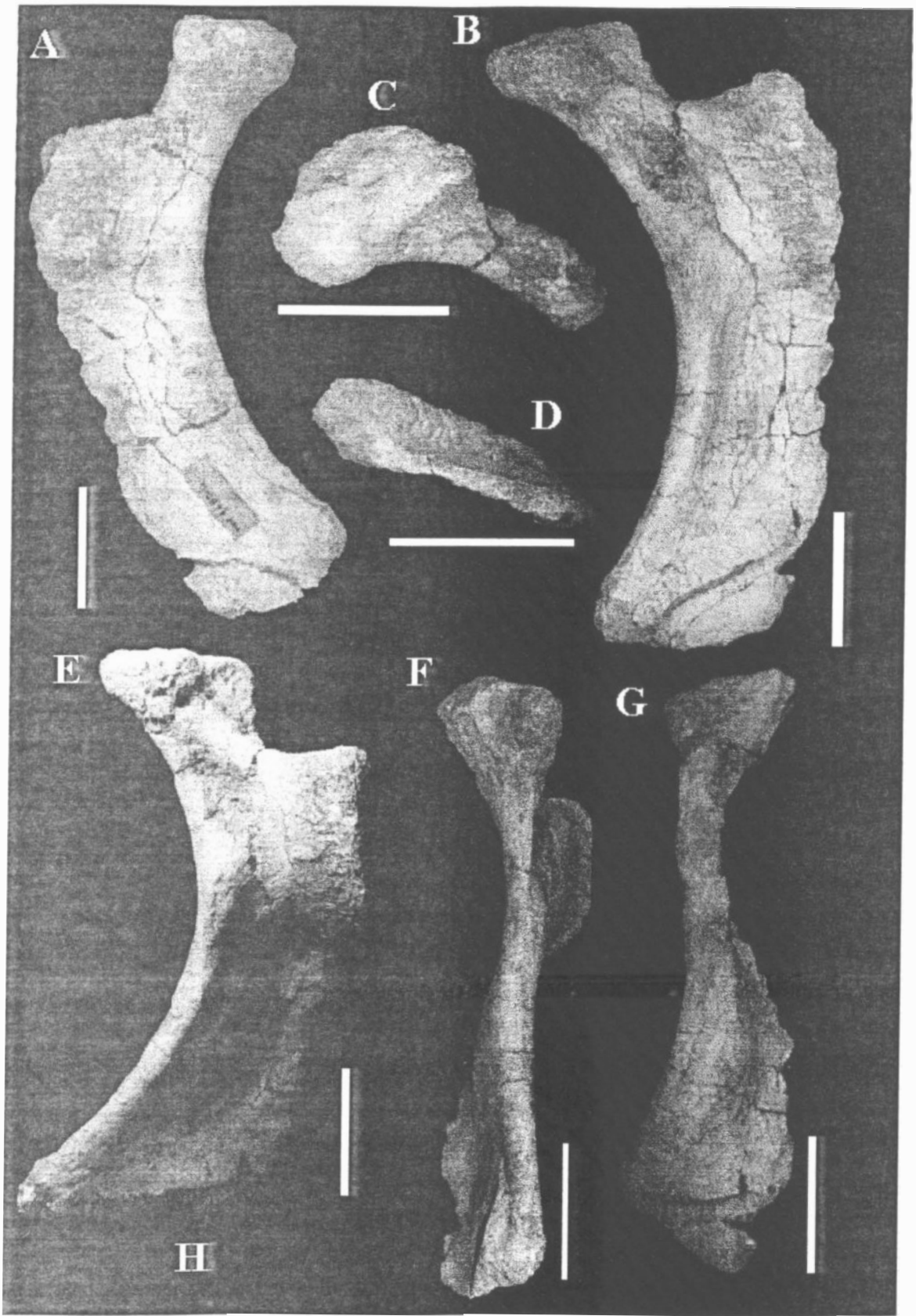


Fig. 100. Right ischium MCT 1689-R in: A) superior; B) inferior; C) proximal 9iliac); D) distal; E) inferior (low light angle); F) posterior and G) anterior (pubic) views. Scale bar = 10 cm.

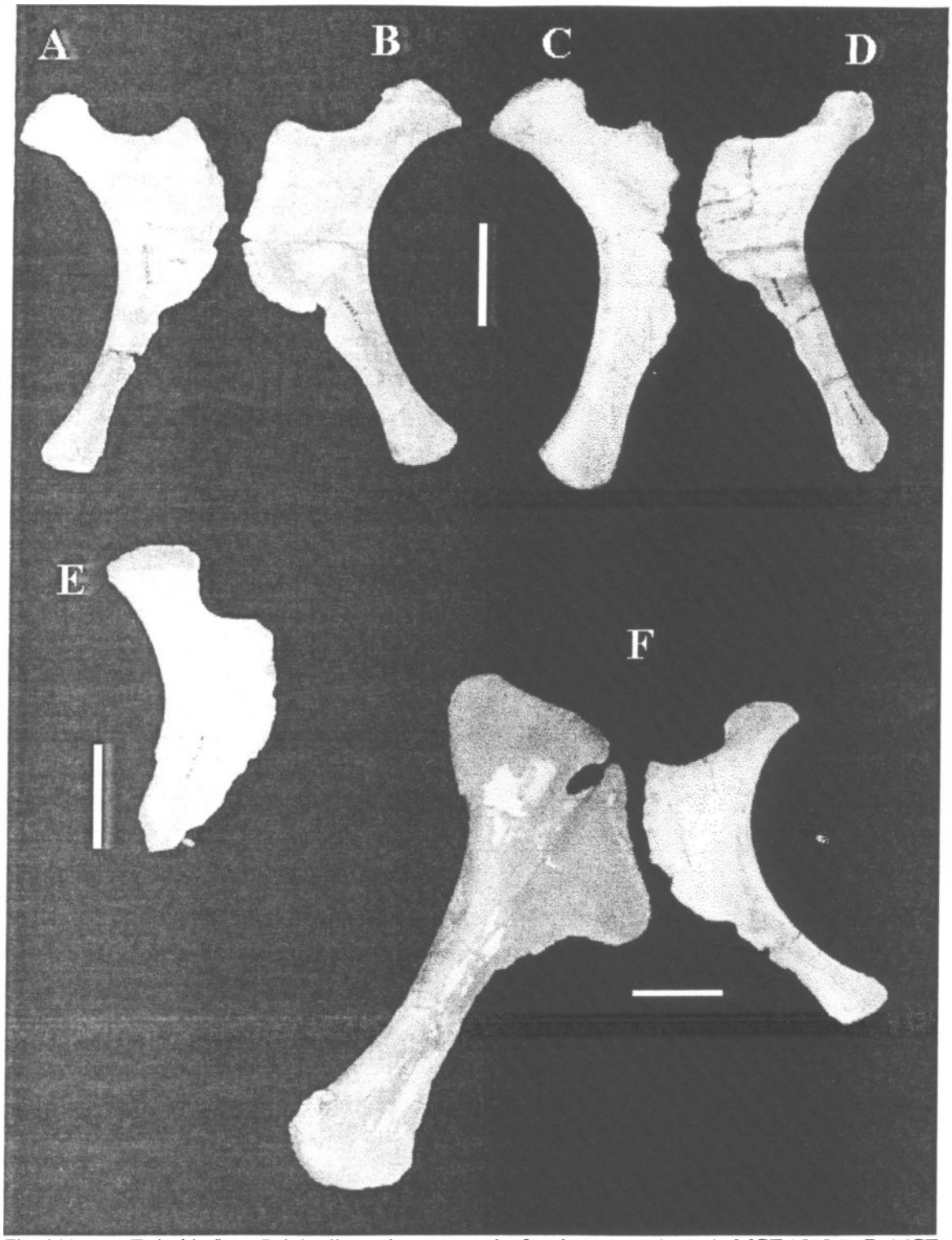


Fig. 101. A to E) ischia from Peirópolis, at the same scale, for size comparison: A) MCT 1585-R; B) MCT 1586-R; C) MCT 1661-R; D) MCT 1655-R and E) MCT 1654-R. All in superior view.
F) Associated left pubis MCT 1592-R and left ischium MCT 1585-R in lateral view. Both from "Serra da Galga". Both at the same scale. Scale bar = 10 cm.

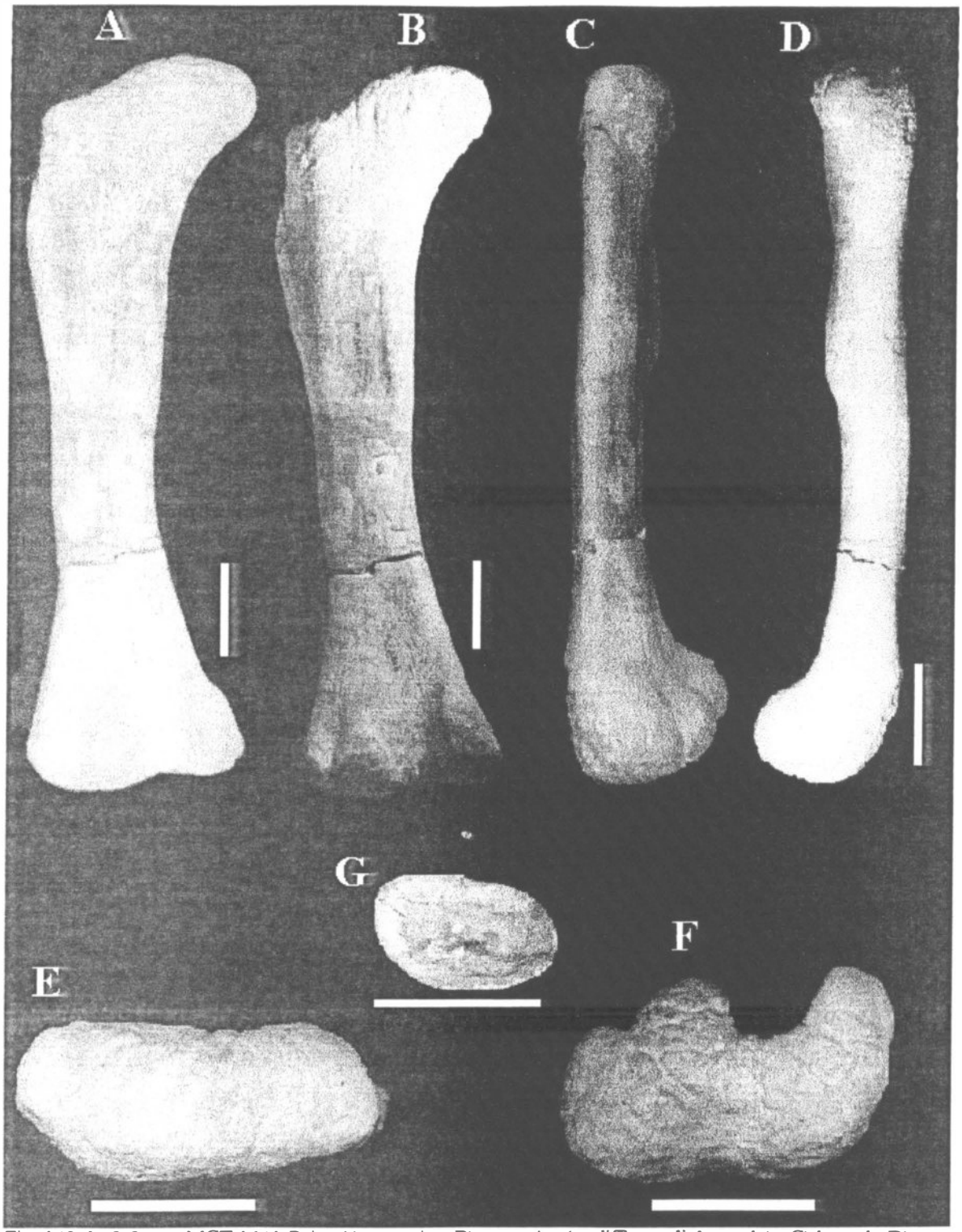


Fig. 102. Left femur MCT 1601-R in: A) posterior; B) posterior (at different light angle); C) lateral; D) medial; E) proximal and F) distal views. G) cross-section of the shaft. Scale bar = 10 cm.

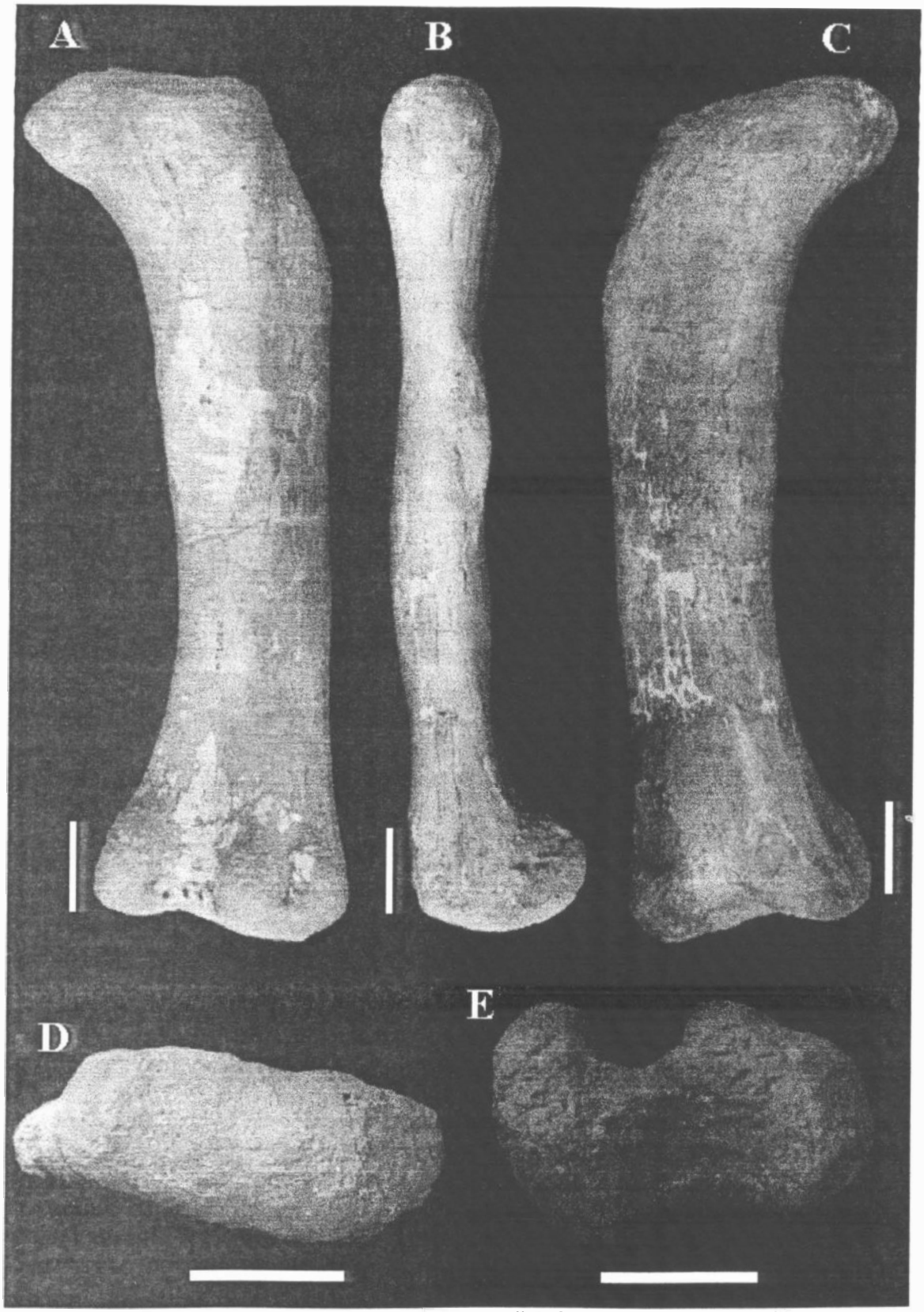


Fig. 103. Right femur MCT 1692-R in: A) posterior; B) medial; C) anterior; D) proximal and E) distal views. Scale bar = 10 cm.

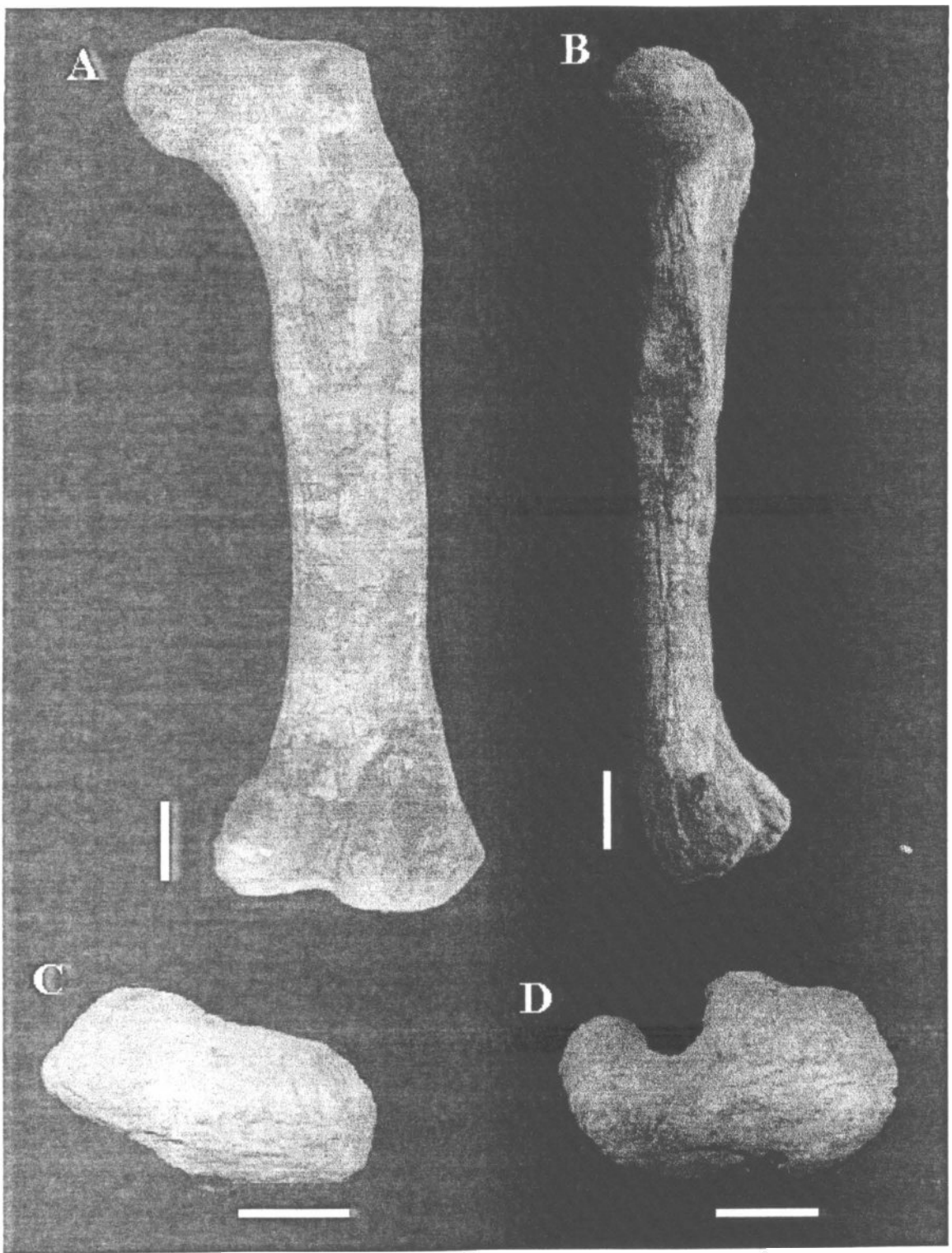


Fig. 104. Right femur MCT 1693-R in: A) posterior; B) medial; C) proximal and D) distal views. Scale bar = 10 cm.

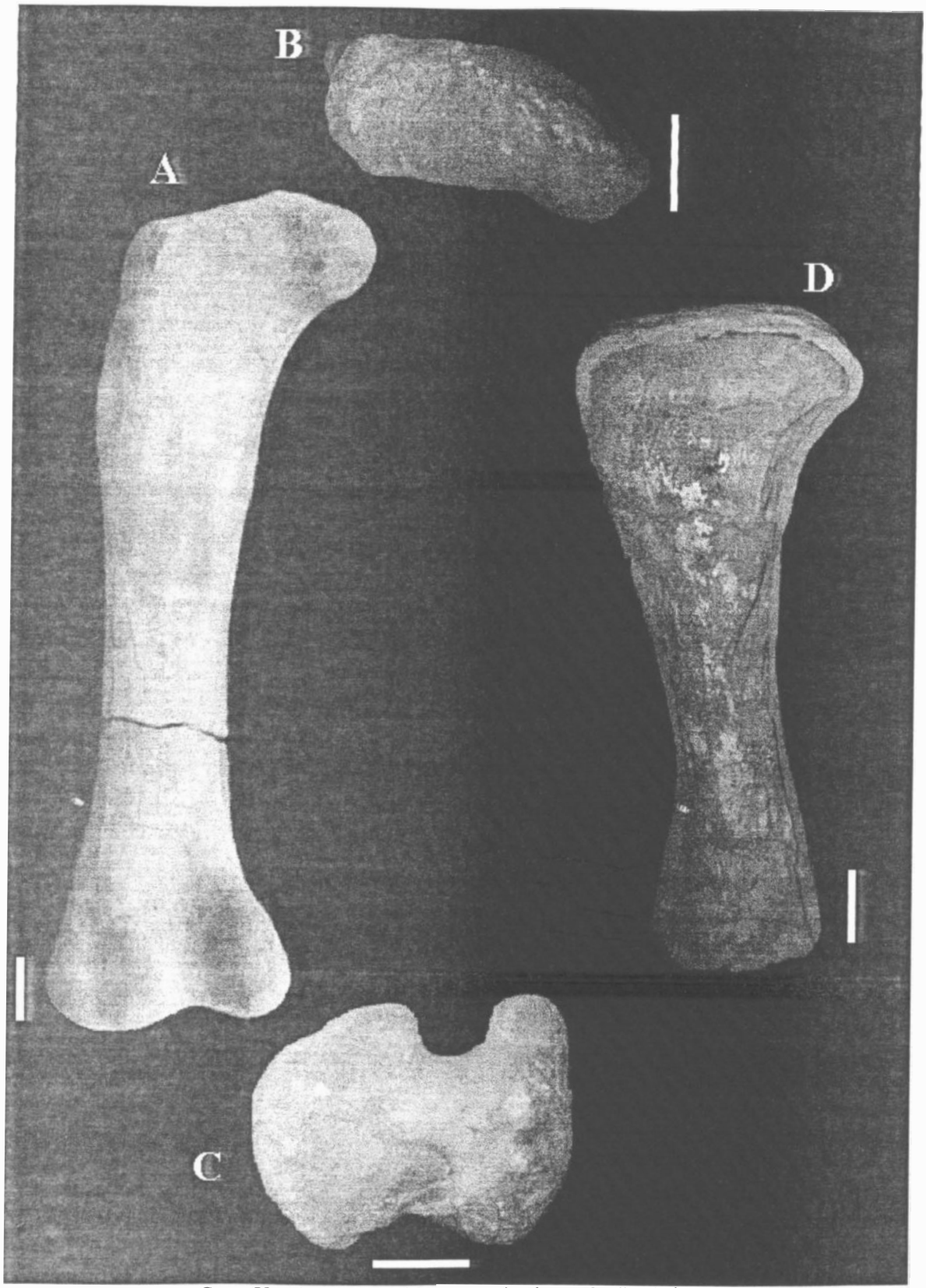


Fig. 105. Left femur MCT 17??-R in: A) posterior; B) proximal and C) distal views. Left femur MCT 1694 IN: D) posterior view. Scale bar = 10 cm.

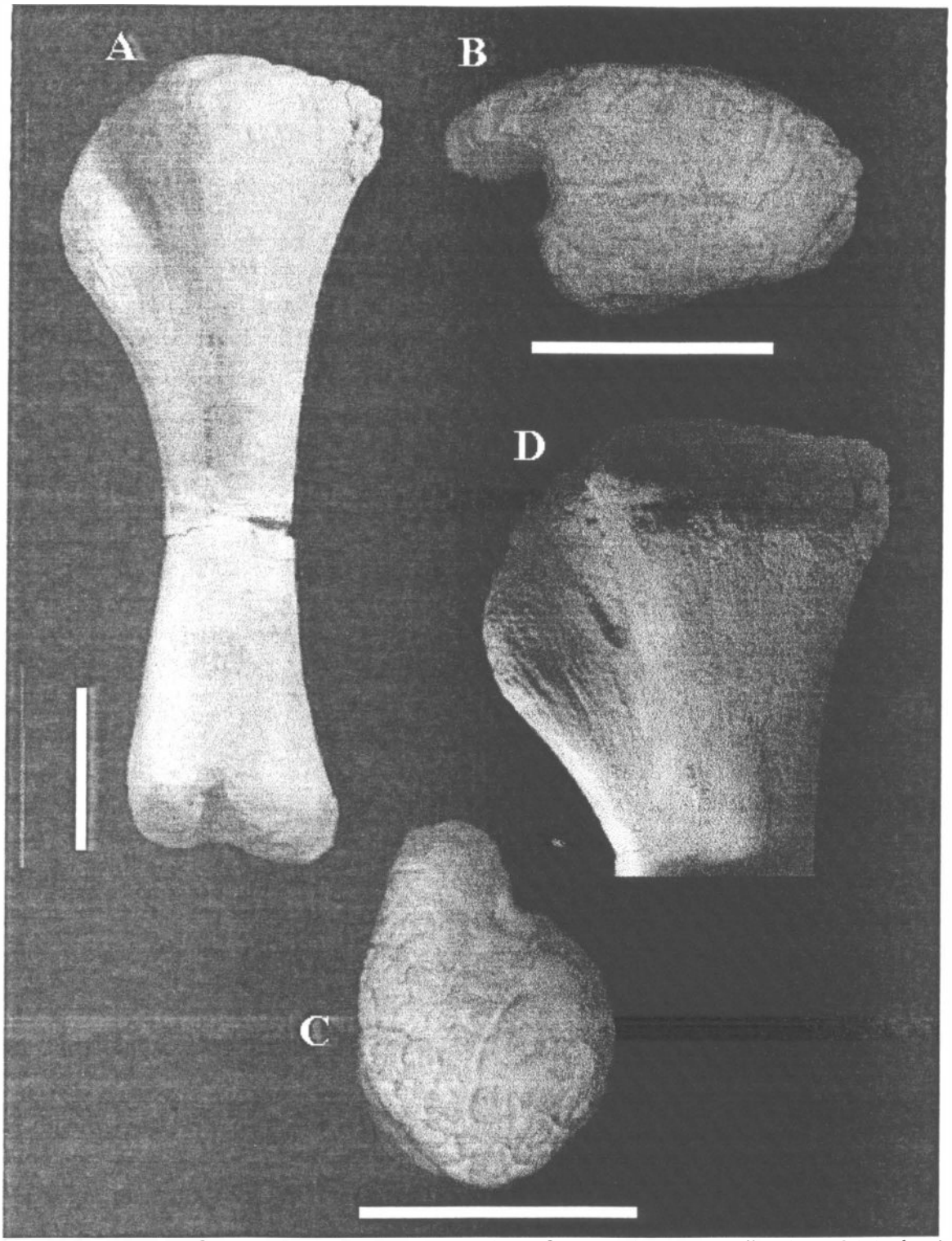


Fig. 106. Left tibia MCT 1587-R in: A) lateral; B) proximal; C) distal views. D) medial view of tibial head. showing the digitiform concavity. Scale bar = 10 cm.

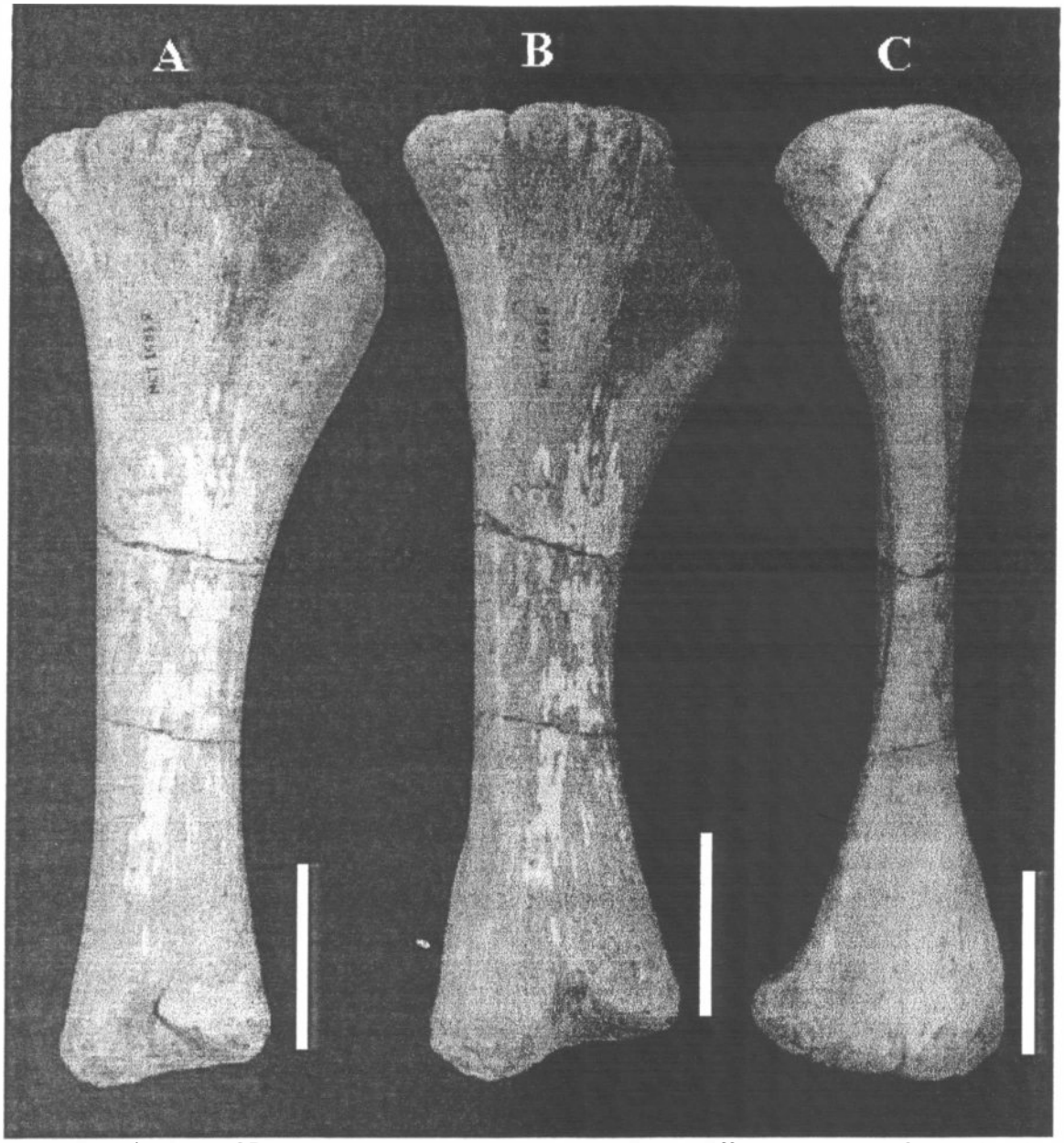


Fig. 107. Right tibia MCT 1681-R in: A) lateral; B) lateral (at slightly different angle) and C) anterior views. Scale bar = 10 cm.

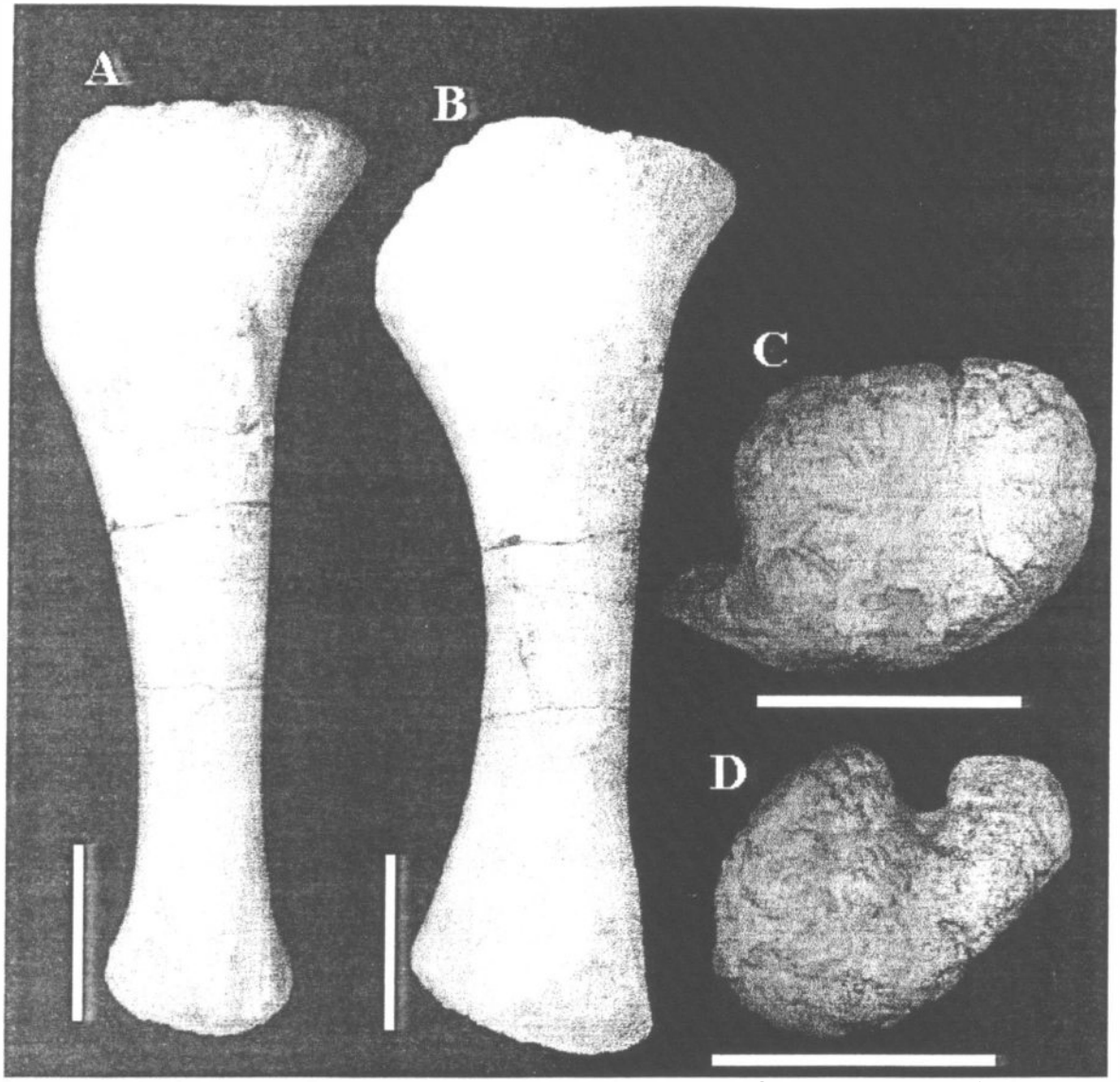


Fig. 108. Right tibia MCT 1681-R in: A) medio-posterior; B) posterior; C) proximal and D) distal views. Scale bar = 10 cm.

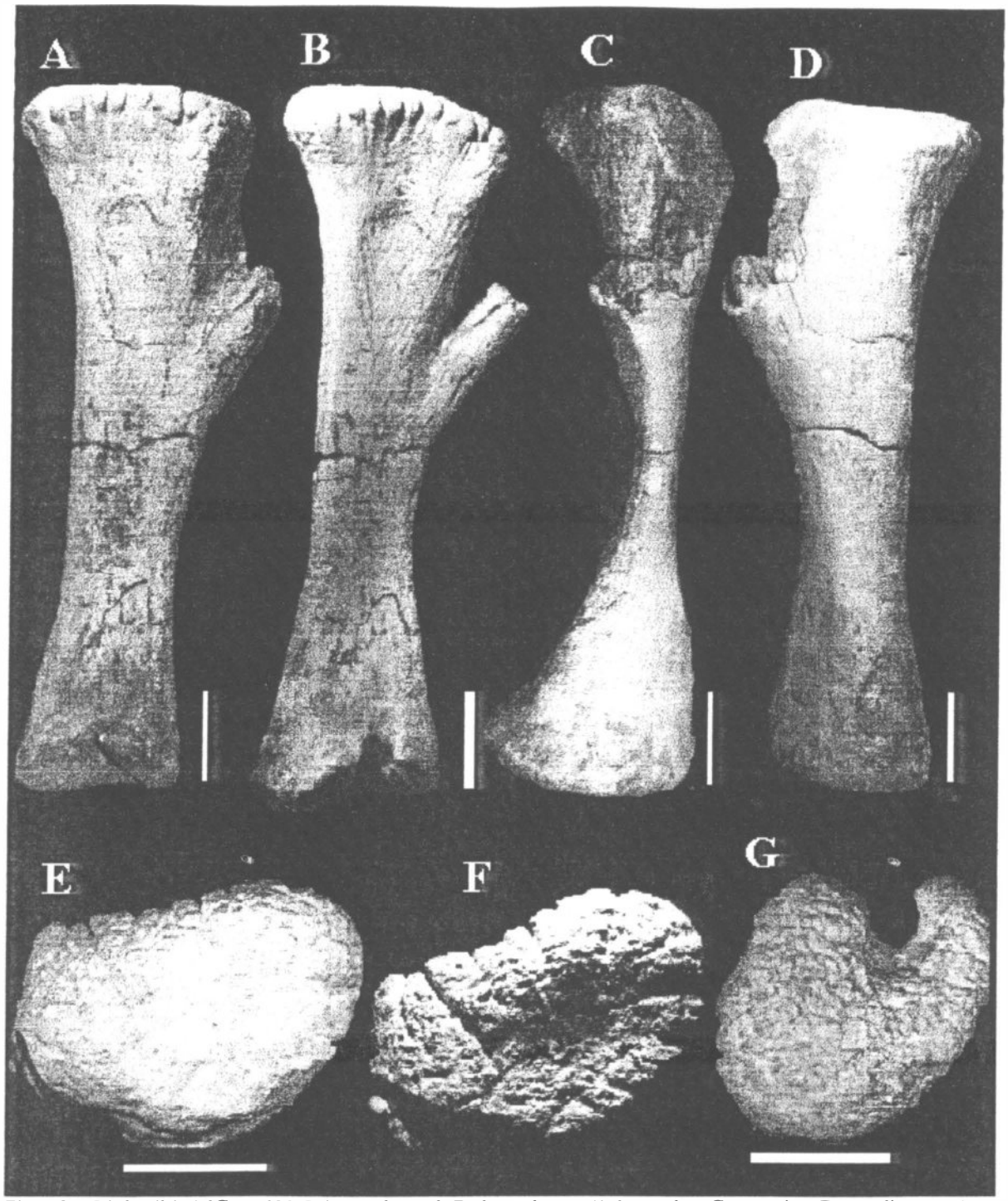


Fig. 109. Right tibia MCT 1683-R in: A) lateral; B) lateral (low light angle); C) anterior; D) medio-anterior; E) proximal; F) proximal (low light angle) and G) distal views. Scale bar = 10 cm.

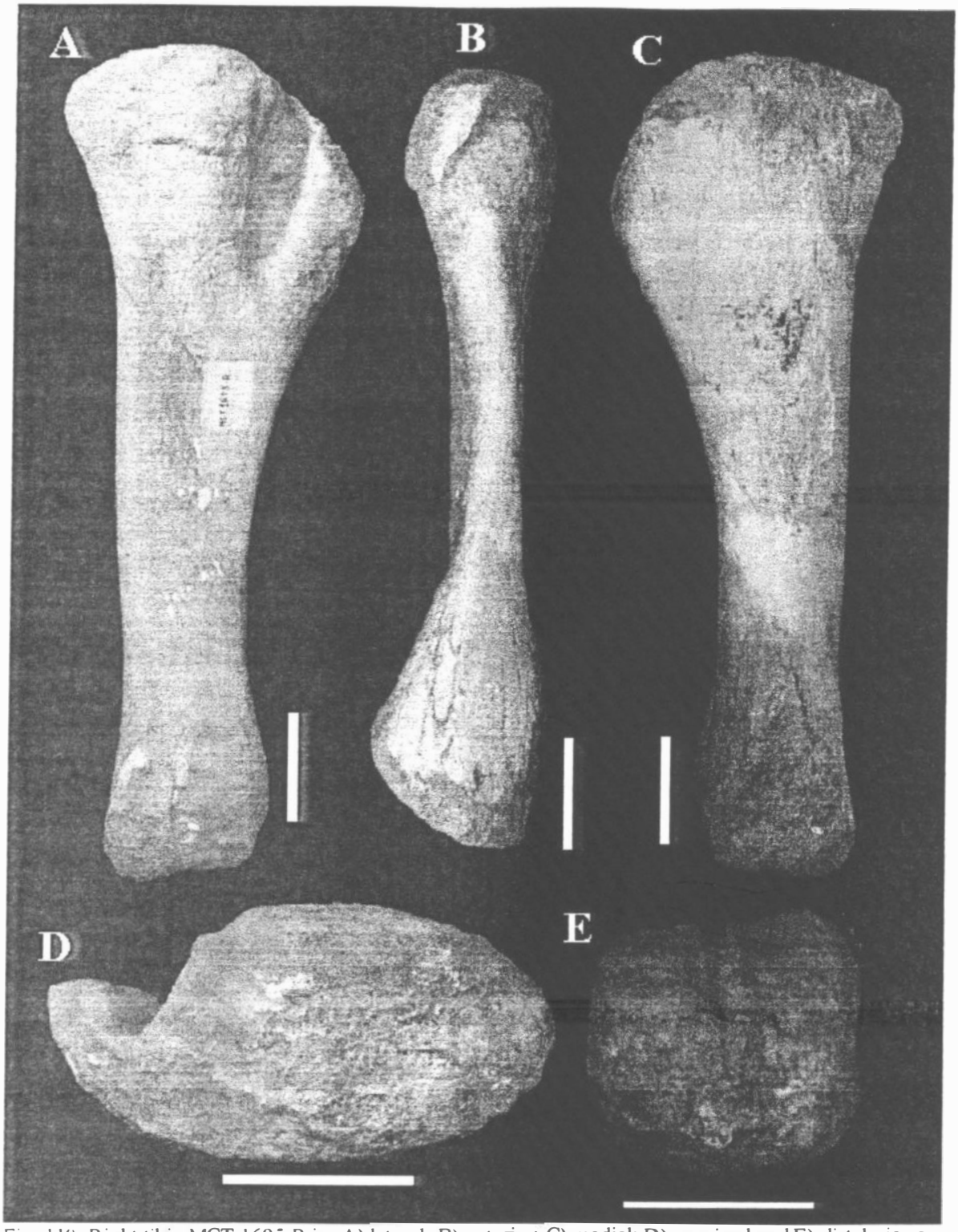


Fig. 110. Right tibia MCT 1695-R in: A) lateral; B) anterior; C) medial; D) proximal and E) distal views. Scale bar = 10 cm.

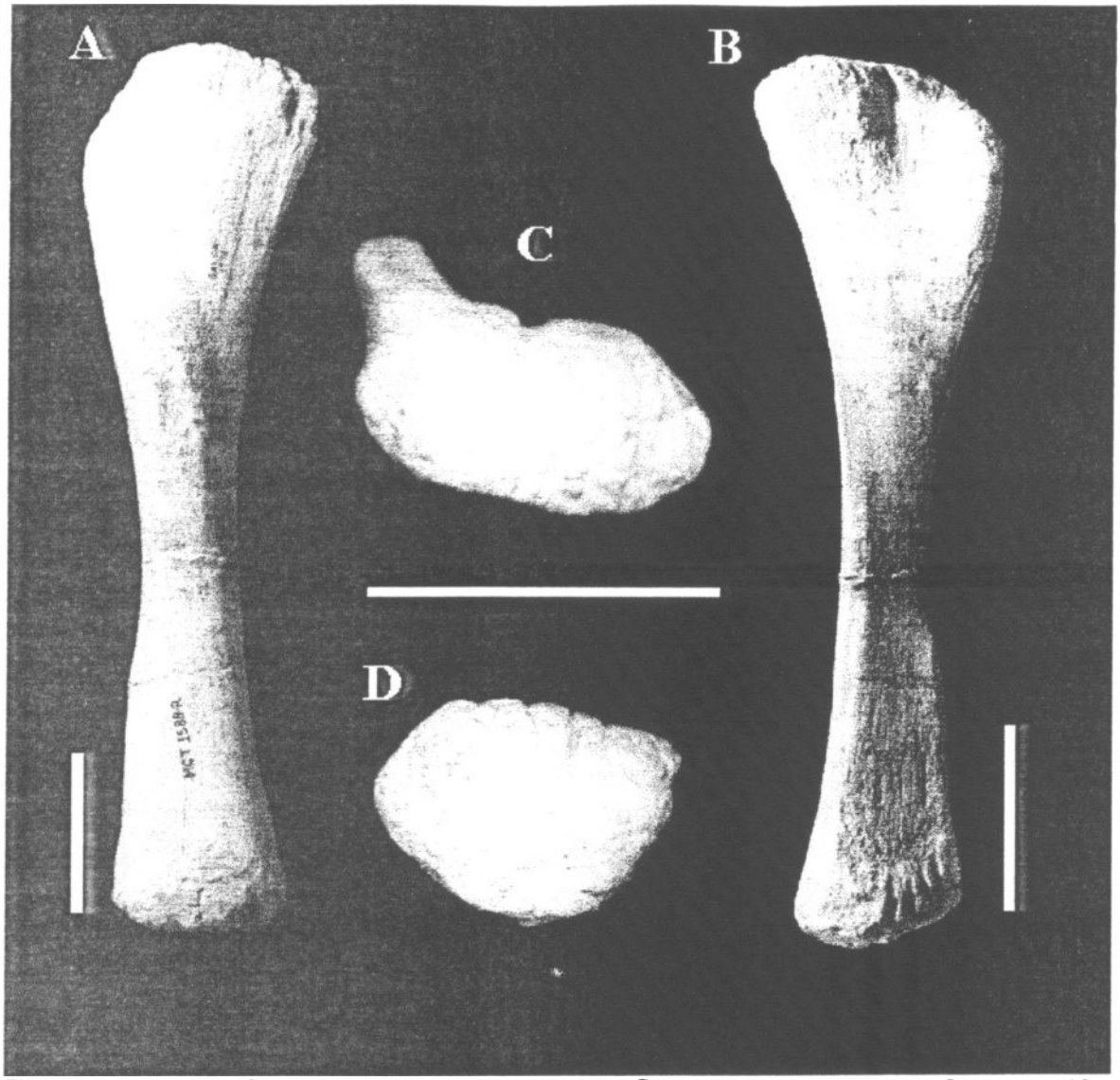


Fig. 111. Left fibula MCT 1588-R in: A) lateral; B) medial; C) proximal; D) distal views. Scale bar = 10 cm.

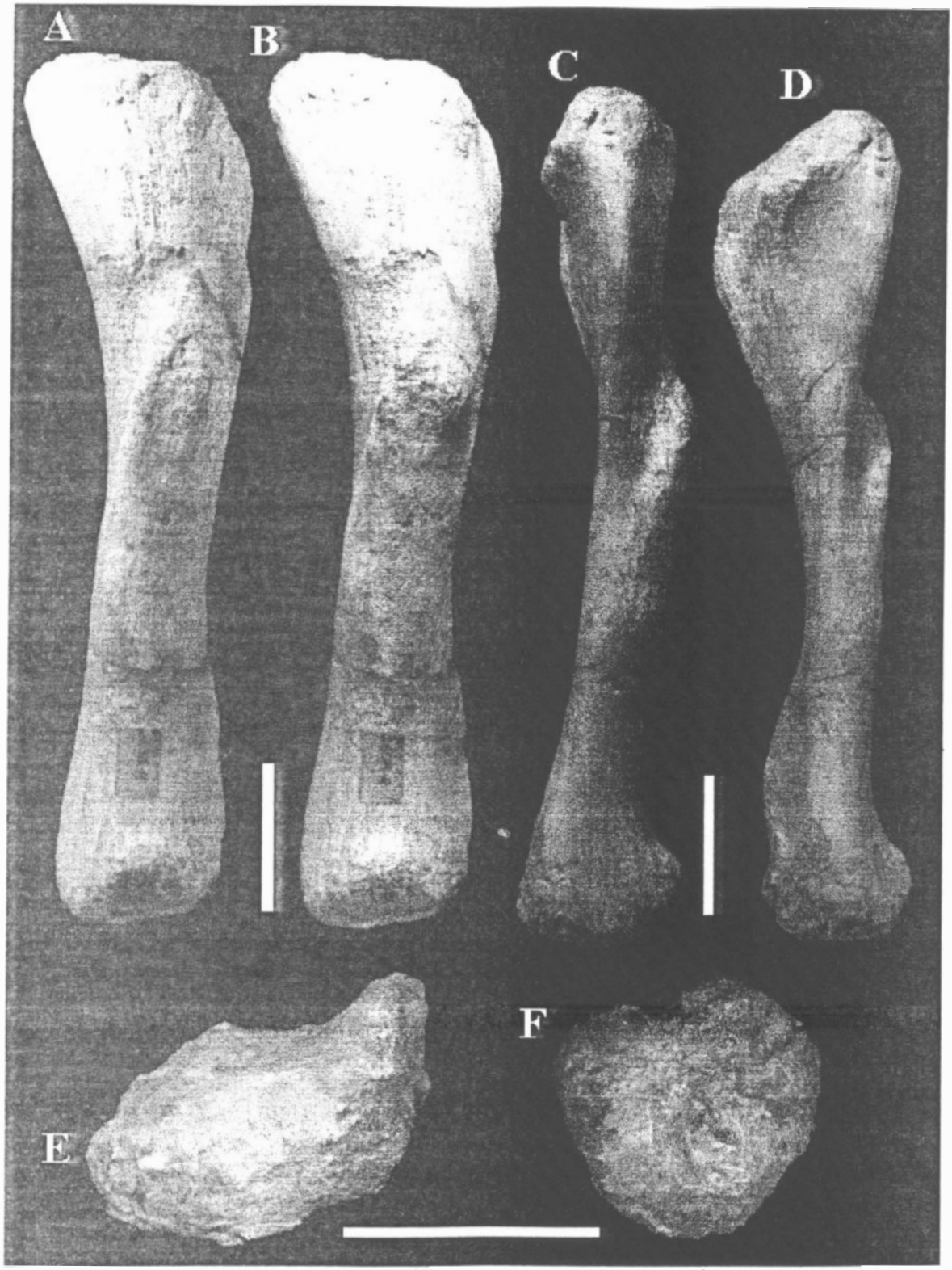


Fig. 112. Right fibula MCT 1608-R in: A) lateral; B) lateral (low light angle); C) posterior; D) medio-posterior; E) proximal; F) distal views. Scale bar = 10 cm.

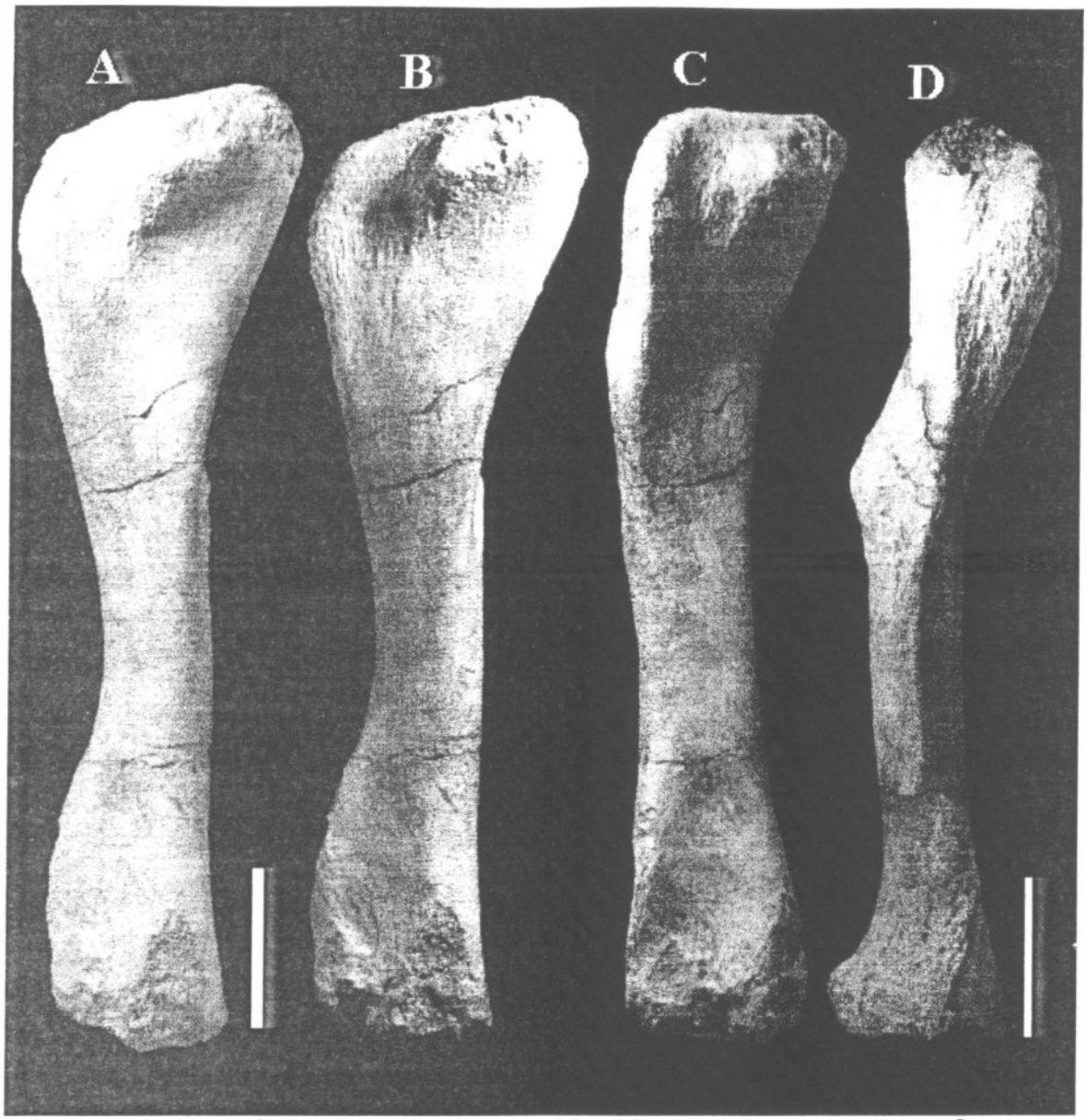


Fig. 113. Right fibula MCT 1608-R in: A) medial (anterior light); B) medial (posterior light); C) antero-medial and D) anterior views. Scale bar = 10 cm.

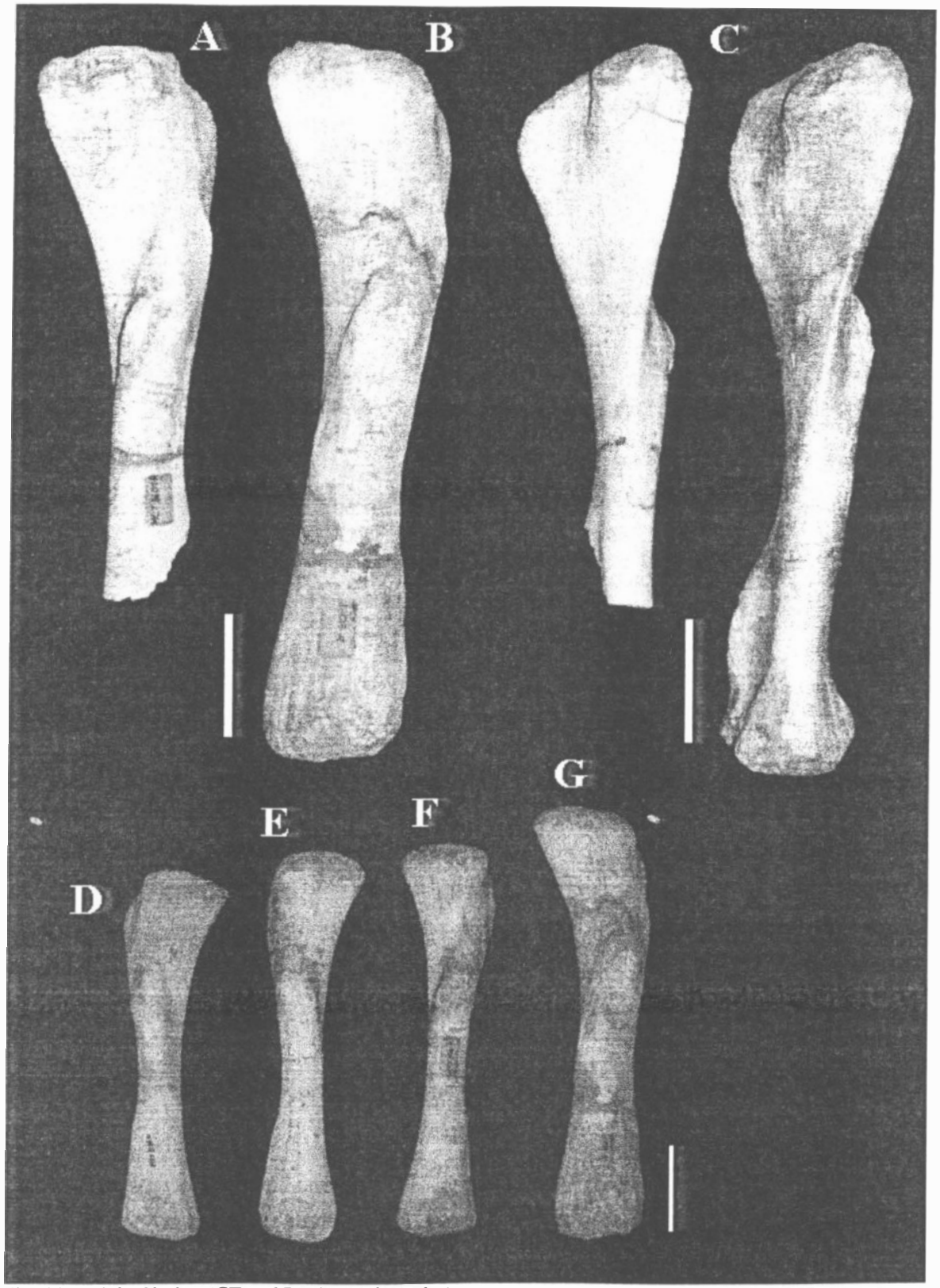


Fig. 114. Right fibula MCT 1607-R in: A) lateral view.

Right fibula MCT 1608-R in: B) lateral view, for comparison; C) the two fibulae in medio-posterior view for comparison.

Fibulae from Peirópolis, for size comparison: D) MCT 1588-R; E) MCT 1657-R; F) MCT 1660-R and G) MCT 1608-R. All lateral views, and at the same scale. Scale bar = 10 cm.

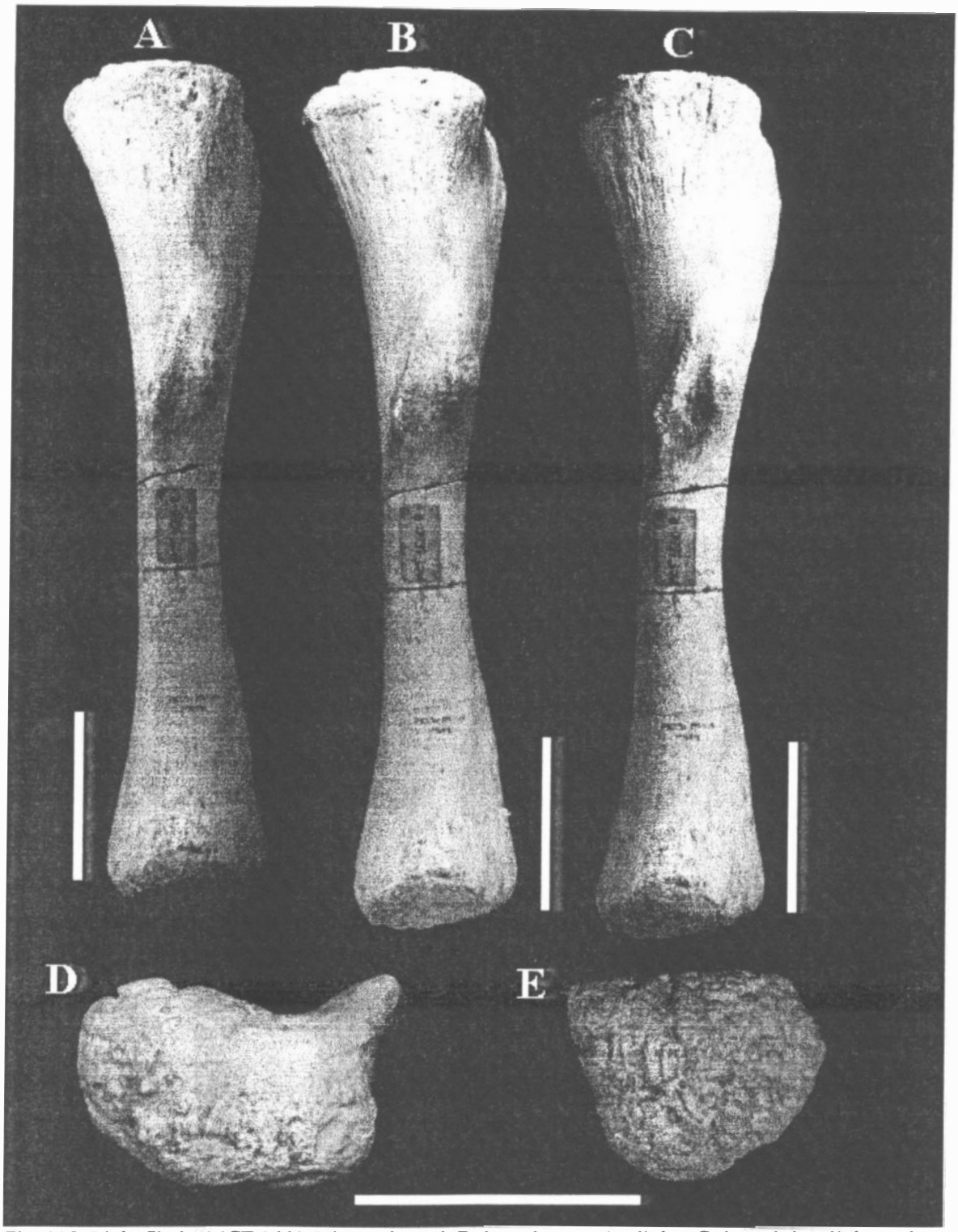


Fig. 115. Right fibula MCT 1660-R in: A) lateral; B) lateral (posterior light); C) lateral (low light angle to show divided lateral trochanter); D) proximal and E) distal views. Scale bar = 10 cm.

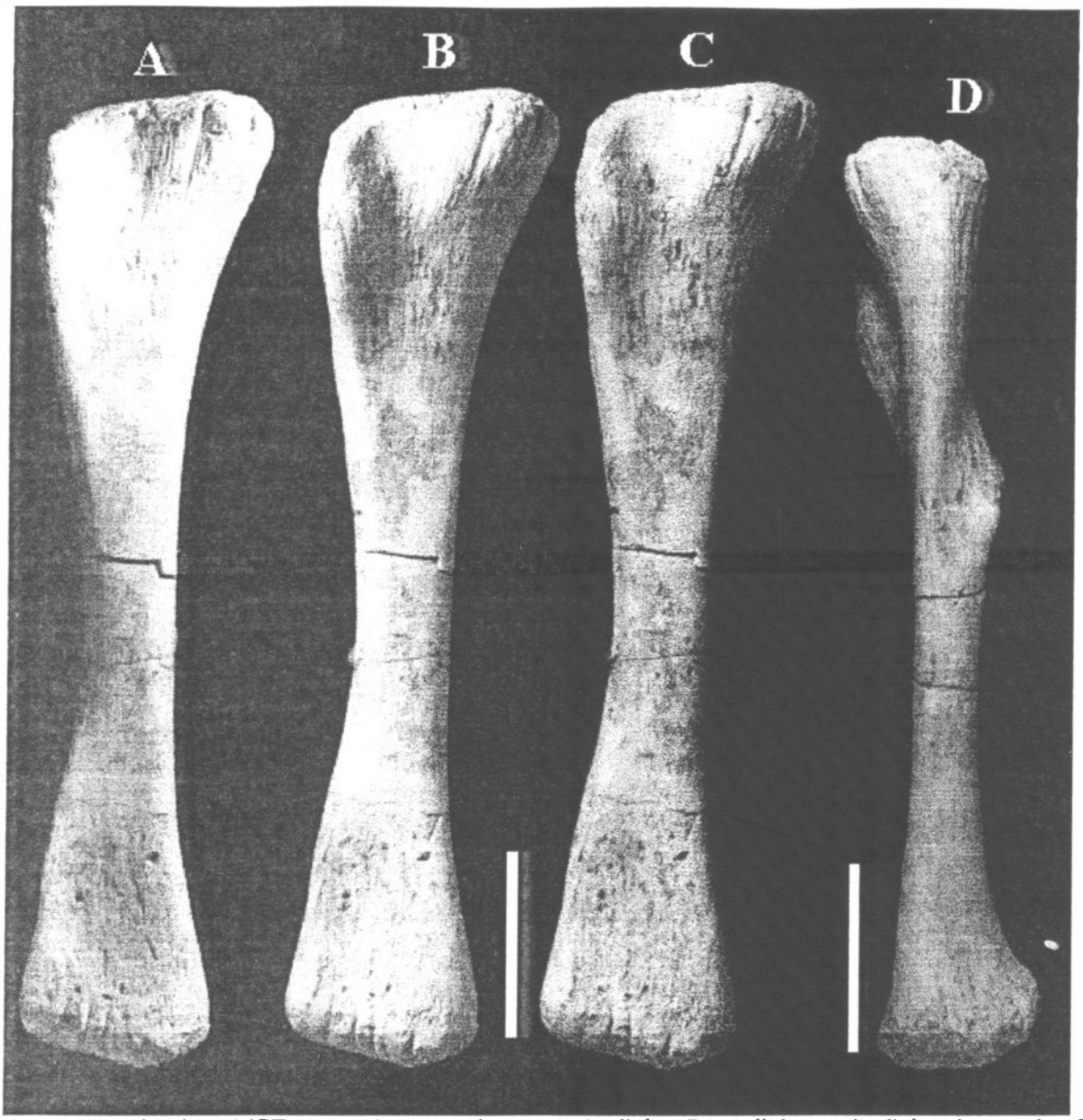


Fig. 116. Right fibula MCT 1660-R in: A) medial (posterior light); B) medial (anterior light – low angle); C) medial (anterior light) and D) posterior views. A, B, and C to the same scale. Scale bar = 10 cm.

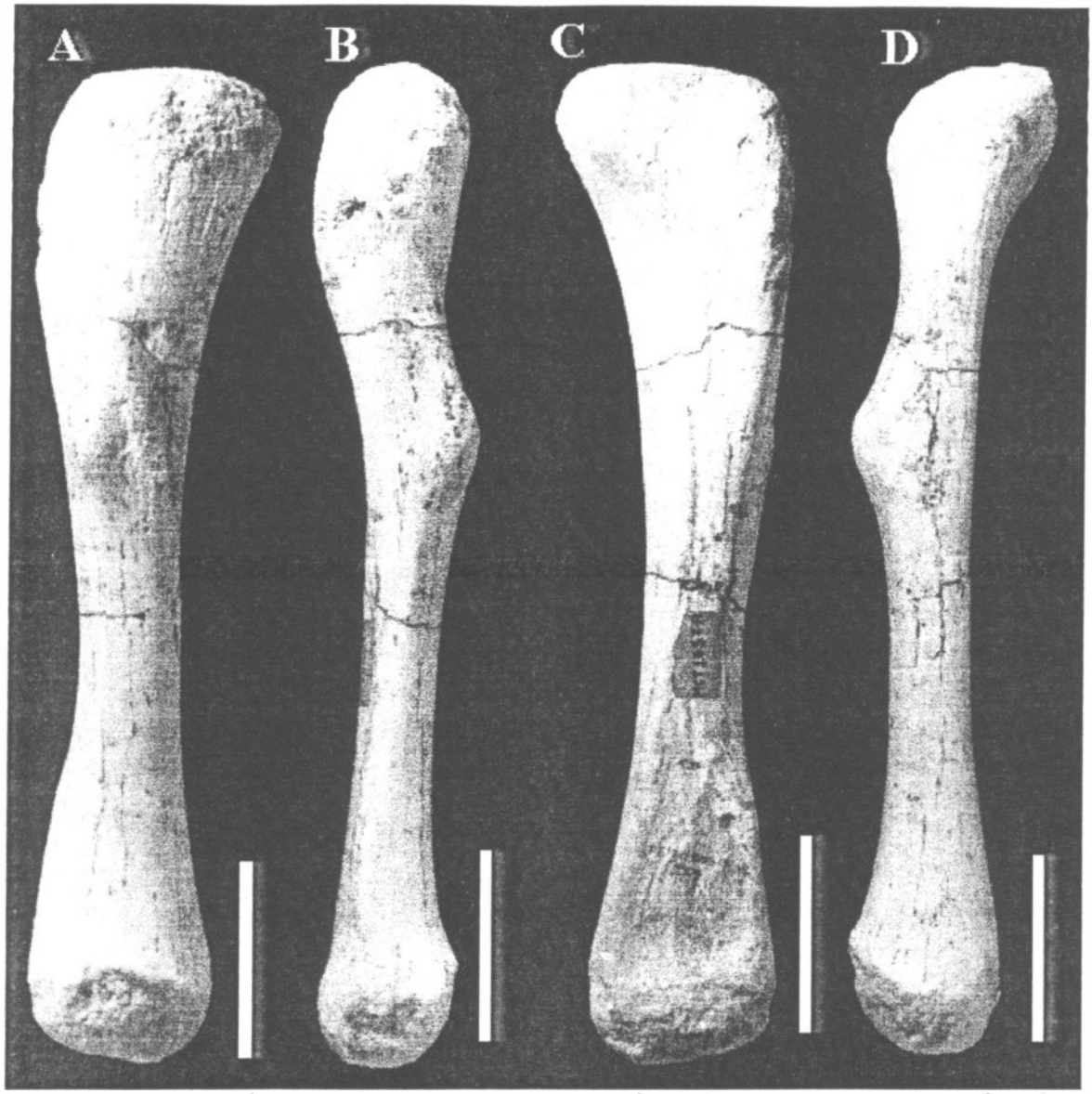


Fig. 117. Left fibula MCT 1657-R in: A) lateral; B) anterior; C) medial and D) posterior views. Scale bar = 10 cm.

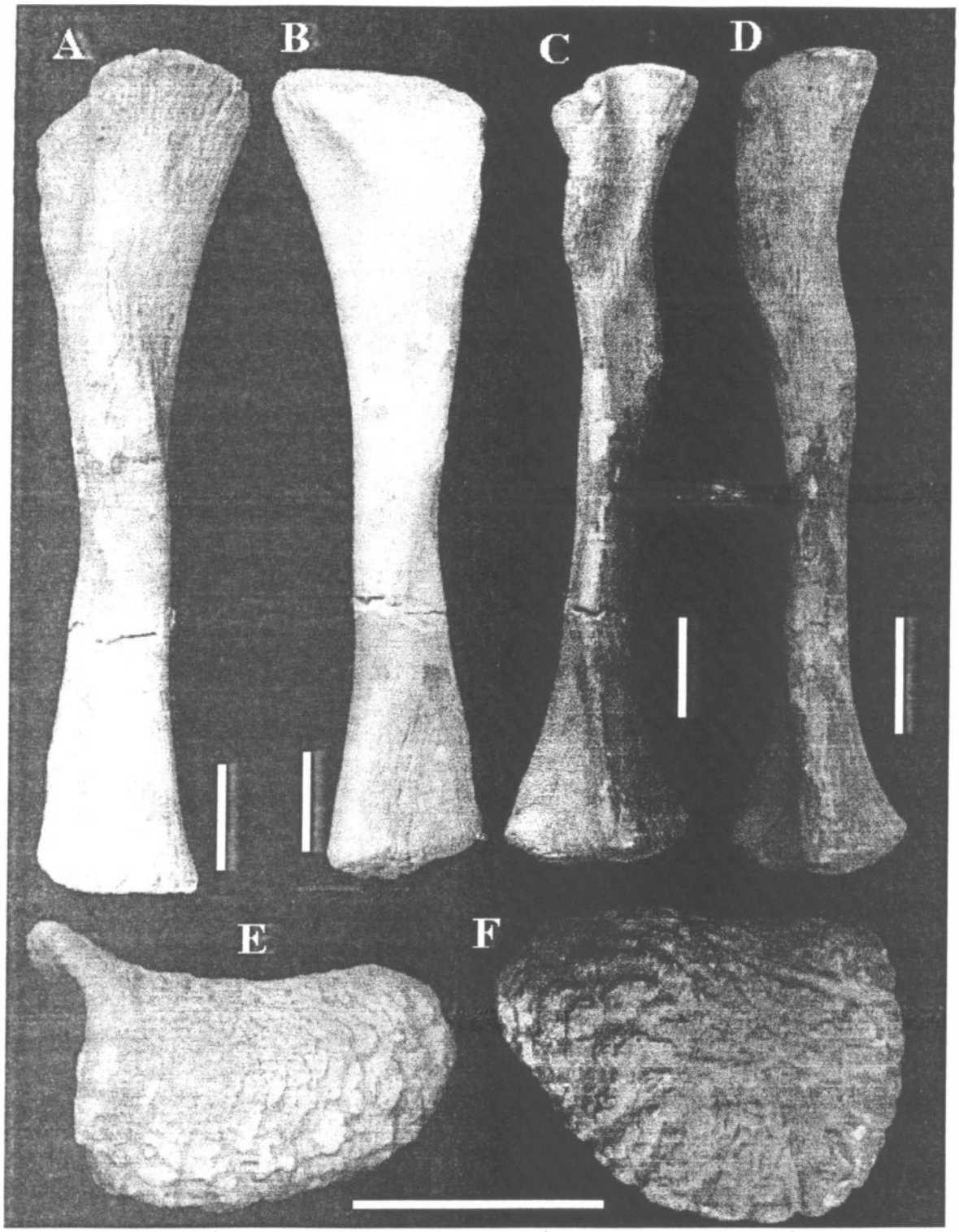


Fig. 118. Left fibula MCT 1696-R in: A) lateral; B) medial; C) anterior; D) anterior (slightly different angle; E) proximal and F) distal views. Scale bar = 10 cm.

APPENDIX

1. MUSEUMS AND RESEARCH INSTITUTIONS ABBREVIATIONS

DNPM – Departamento Nacional de Produção Mineral, Rio de Janeiro - Brazil

GP-RD – Departamento de Geociências da Faculdade de Filosofia, Ciências e Letras de São José do Rio Preto – São Paulo - Brazil

ISI – Geology Museum, Indian Statistical Institute, Calcutta - India

MACN – Museo Argentino de Ciencias Naturales Bernardino Rivadavia - Buenos Aires – Argentina

MAL – Malawi Department of Antiques - Malawi

MCNA – Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz - Spain

MCT – Museu de Ciências da Terra – Rio de Janeiro - Brazil

MJG – Museo J. Gerholdt, Ingeniero Jacobacci, Río Negro - Argentina

MLP – Museo de La Plata – La Plata – Buenos Aires - Argentina

MN – Museu Nacional – Universidade Federal do Rio de Janeiro, Rio de Janeiro - Brazil

MPCA – Museo Provincial Carlos Ameghino, Ciopolleti, Río Negro - Argentina

MUCPv - Museo de Geología e Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina

PVL – Fundación Instituto Miguel Lillo, Tucumán – Argentina

PVPH – Museo Carmen Funes, Plaza Huincul, Neuquén - Argentina

SAM – South African Museum

USNM – United States National Museum - Smithsonian Institution – Washington DC

ZPAL – Institute of Paelobiology, Polish Academy of Sciences, Warsaw

2. MORPHOLOGICAL ABBREVIATIONS

SCAPULA

acr - acromion
cor - art mg coracoidal articular margin
cor art sf - coracoidal articular surface
cvx sf - blade convex surface
exp - upper expansion
gl - glenoid
gl gr - glenoidal groove
ind - scapular indentation
m. ser - muscle scar for *m. serratus*
med prm - medial prominence
sc bl - scapular blade
sc pl - scapular plate

CORACOID

ant bd - anteromedial border
ant prt - anterior protuberance
co fo - coracoidal foramen
conc fs - concave fossa
conc li - concave curved line
gl - glenoid
ind - indentation
obl el - oblique elevation
sc art mg - scapular articular margin
st li - suture line

STERNAL PLATE

ant vnt rdg - antero-ventral ridge
conc - shallow concavity
lat ant prc - latero-anterior process
trv rdg - transverse ridge

HUMERUS

cvx el - semicircular convex elevation
dp cr - deltopectoral crest
gl cnd - glenoidal condyle
lng prm - longitudinal prominence
m cbb - concavity for *m. coracobrachialis brevis*
m. ld - posterior elevation for *m. latissimus dorsi*
m. scha - insertion for *m. scapulohumeralis anterior*
pos cnd rdg - posterior supracondylar ridges
rd cnd - radial condyle
ul cnd - ulnar condyle

ULNA

ant exp - greater or anterior expansion
blg m. -bulge for *m. extensor digitorum comunis* or *m. extensor carpi ulnaris*
dst exc - distal excavation
lat ex - lesser of lateral expansion
lng rdg - longitudinal ridge
md conc - medial concavity (for *m. flexor carpi ulnaris*)
ol - olecranon
rd fs - radial fossa
tr - triangular area

RADIUS

dbl rdg - double ridge
dst art - distal articular area
dst lat exp - distal lateral expansion
el - small elevation at end of *interosseus* ridge
ios - *interosseus* ridge
ios enl - enlargement of *interosseus*
m.bi - elevation for *m. biceps brachialis inferior*
med el - medial elevation
med prj - medial projection
mic - microridge
sc rdg - second ridge
str - subtriangular depression

PUBIS

il ped - iliac pedicle
is ped - ischial pedicle
lat rdg - lateral ridge
m. amb - scar for *m. ambiens*
pu apr - pubic apron
pub act - acetabular portion of pubis
pu fo - pubic foramen
pu sym - pubic symphysis
sl - slope

ISCHIUM

act - acetabulum
dst - distal shaft
il ped - iliac pedicle
is sym - ischial symphysis
lat prc - lateral process
med r - medial reentrance
pu ped - pubic pedicle

FEMUR

fib cnd - fibular condyle
fo trc - fourth trochanter
gr trc - grater trochanter
lat blg - lateral bulge
tb cnd - tibial condyle

TIBIA

ant cnd - anterior condyle
cnc - concavity at head of tibia
cn cr - cnemial crest
dgt - digitiform depression
med el - medial elevation
nt - notch
pos cnd - posterior condyle

FIBULA

ant trc - anterior trochanter
fib cr - fibular crest
lat trc - lateral tuberosity/trochanter
obl rdg - oblique ridge
st - stalk
tb art - tibial articular surface

3. SYNAPOMORPHIES

A list of synapomorphies of the Sauropoda (WILSON & SERENO, 1998):

SAUROPODA

1. obligatory, quadrupedal posture with columnar limbs and short metapodials
2. sacral vertebral number four or more
3. Humeral deltopectoral crest low
4. Olecranon reduced or absent
5. Ulna proximal end triradiate, with deep radial fossa
6. Radial distal condyle subrectangular with flat posterior margin for ulna.
7. Ilium with low ischial peduncle
8. Ischial shaft equal to, or longer than pubic shaft
9. Ischial shaft with dorsoventrally flattened distal end
10. Femoral shaft with elliptical cross section, long axis of ellipse oriented mediolaterally
11. Femoral fourth trochanter developed as a low crest
12. Astragalar fossa and foramina at base of ascending process absent
13. Distal tarsals 3 and 4 absent or unossified
14. Metatarsal I and V with proximal end subequal in area to that of metatarsal II and IV
15. Metatarsal V length at least 70 percent that of metatarsal IV
16. Pedal digit I ungual enlarged.
17. Pedal digit I ungual deep and narrow (sickle shaped)

EUSAUROPODA

18. External nares retracted posterodorsally
19. Snout with stepped anterior margin
20. Antorbital fossa absent
21. Maxillary border of external naris long.
22. Anterior process of prefrontal absent
23. Squamosal-quadratojugal contact absent
24. Anterior ramus of quadratojugal elongate, distally expanded
25. Infraorbital region of skull shrtened anteroposteriorly
26. Supratemporal region of cranium shortened anteroposteriorly
27. Supratemporal fossa broadly exposed laterally
28. Quadrate shaft with elongate posterior fossa
29. Palatine lateral ramus narrow
30. Dentrary ramus, maximum depth of anterior end approximately 150 percent minimum depth of ramus
31. Tooth rows broadly arched anteriorly
32. Spatulate crowns
33. Tooth enamel with wrinkled texture
34. Tooth crown overlap
35. Precise crown-to-crown occlusion
36. V-shaped wear facets (interdigitating occlusion)
37. Cervical vertebrae 13 or more in number

38. Cervical centra opisthocoelus
39. Mid-cervical neural arches deep, greater than centrum diameter
40. Dorsal neura spines broader transversely than anteroposteriorly
41. Distal chevrons with anterior and posterior projections
42. Block-shaped carpals
43. Manual phalanges on digits II and III reduced (digital formula 2-2-2-2-2 or lower)
44. Manual phalanges (other than unguals) broader than long
45. Iliac blade with semicircular dorsal margin and expanded pre-acetabular process
46. Pubic apron canted posteromedially
47. Tibial cnemial crest projecting laterally
48. Tibial posteroventral process reduced
49. Fibular lateral trochanter
50. Metatarsal III length 25 percent or less that of tibia
51. Metatarsal I minimum shaft width greater than that of metatarsals II-IV
52. Metatarsals with spreading configuration
53. Pedal phalanges (other than unguals) short
54. Pedal digit I ungual equal to or longer than metatarsal I
55. Pedal digits II-IV, penultimate phalanges rudimentary or absent
56. Pedal digits II-III with sickle shaped unguals
57. Pedal digit IV ungual rudimentary or absent

Barapasaurus + *Omeisaurus* + NEOSAUROPODA

58. Posterior cervical and anterior dorsal neural arches with interprezygapophyseal lamina.
59. Anterior dorsal centra opisthocoelous
60. Middle and posterior dorsal neural arches with composite lateral lamina (spinodiapophyseal plus supraprezygapophyseal).
61. Sacricostal yoke
62. Fibula with broad triangular articular scar for tibia
63. Astragalar posterior fossa divided by crest
64. Pedal unguals asymmetrical (canted ventrolaterally in articulation)

Omeisaurus + NEOSAUROPODA

65. Frontal excluded from supratemporal fossa
66. Supratemporal fenestra, long axis, oriented transversely
67. Dentraru tooth count 17 or fewer, teeth restricted anterior of the antorbital fenestra.
68. Presacral pleurocoels deep, invaginated
69. Cervical pleurocoels divided
70 (3). Dorsal vertebral number 12 or fewer
2 (2). Sacral vertebral number five or greater (at least one dorsosacral added)
71. Cervical rib shafts positioned below centra
72. Acromion more than 150% of the minimum width of scapular blade
73. Metatarsals II and Iv with minimum tranverse shaft diameters 65 per cent or less than that of metatarsals I and II

NEOSAUROPODA

74. Preantorbital fenestra
75. Ventral process of postorbital broader transversely than anteroposteriorly
76. Jugal-ectopterygoid contact absent
77. External mandibular fenestra closed
78. Crown denticles absent
79. Carpal number two or fewer
80. Metacarpals bound (long intermetacarpal articular surfaces)
81. Metacarpals, proximal end subtriangular, composite proximal articular surface U-shaped
82. Iliac preacetabular blade laterally divergent (width across ilia greater than iliac length)
83. Tibia with subcircular proximal end
84. Astragalar ascending process extends to posterior margin of the astragalus
85. Astragalus wedge-shaped in anterior view

MACRONARIA

86. Middle and posterior dorsal neural spines with transversely flared distal ends
87. Anterior caudal chevrons with open proximal articulation
88. Ischial distal shafts platelike and nearly coplanar

Camarasaurus + TITANOSAURIFORMES

89. External naris, maximum diameter greater than orbital maximum diameter
90. Quadrate fossa deep
91. Surangular depth more than twice depth of the angular
92. Posterior dorsal centra opisthocoelous, convexity present on anterior face of centrum
93. Length of longest metacarpal 45 percent or more that of the radius
94. Metacarpal I subequal in length to metacarpal IV
95. Puboischial contact deep dorsoventrally

TITANOSAURIFORMES

96. Pterygoid lacking dorsomedially oriented basipterygoid hook
97. Dorsal ribs with pneumatic cavities
98. Metacarpal I distal condyle undivided, phalangeal articular surface reduced
99. Iliac preacetabular process semicircular, with posteroventral excursion of its cartilage cap
100. Femur with proximal one-third of shaft deflected medially

SOMPHOSPONDYLI

101. Rudimentary
102. Presacral vertebrae composed of spongy bone
103. Anterior to mid-dorsal neural spines posterodorsally inclined

2(3). Sacral vertebral number six (one dorsosacral added)
104. Scapular glenoid deflected medially

A list of synapomorphies of the Sauropoda (SALGADO *et. al.*, 1997a):

SAUROPODA

1.Opisthocoelous cervical and anterior trunk vertebrae
2(1) Four or more sacral vertebrae
3.Ilium with pubic peduncle much longer than ischiatic articulation
4. Femur nearly straight in lateral view
5. Metatarsals shorter than metacarpals

EUSAUROPODA

6. Anterior trochanter of femur absent
7. Anteroposterior diameter of distal end of tibia subequal/greater than distal width

NEOSAUROPODA

8. Presence of pleurocoels on presacral vertebrae.
2(2) Five of more sacral vertebrae

CAMARASAUROMORPHA

9. Opisthocoelous posterior trunk and sacral centra
10* antero-dorsal edge of neural spine placed anteriorly with respect to anterior root of mid-caudal postzygapophysis.
11. Open haemal canal in anterior caudals
12. Relatively long metacarpals
13. Dorsoventrally extended pubic articulation of ischium

TITANOSAURIFORMES

14(1)* Presence of medial prespinal lamina in posterior trunk vertebrae
15. Neural arches positioned anteriorly in mid- and posterior caudal centra
16(1). Claw on manual digit I reduced or absent
17. Broadly expanded preacetabular lobe of the ilium upwardly directed.
18. Pubic peduncle perpendicular to the sacral axis
19. Presence of a prominent lateral bulge in femur, below greater trochanter.

UNNAMED TAXON I (*Chubutisaurus insignis* + TITANOSAURIA)

7(-). Distal end of tibia broader transversely than anteroposteriorly.

TITANOSAURIA (*Andesaurus delgadoi* + TITANOSAURIDAE)

20. Eye-shaped pleurocoels in trunk vertebrae

21. Posterior trunk vertebrae with ventrally widened, slightly forked infradiapophyseal laminae.

22*. Presence of centro-parapophyseal lamina in posterior trunk vertebrae

23(1). anterior caudals procoelous

24*. Pubis considerably longer than ischium

TITANOSAURIDAE

25*. Absence of huposphene-hypantrum articulation in posterior trunk vertebrae

2(3)*. Six sacral vertebrae

23(2). Anterior caudals strongly procoelous, having "ball and socket" articular faces

26*. Semilunar sternal plates

16(2)*. Claw on manual digit I absent

27* Manual phalanges absent

28*. Preacetabular lobe of ilium nearly horizontal, outwardly projected

UNNAMED TAXON II (Unnamed Taxon III + Unanmed taxon V)

14(2). Medial prespinal lamina formed down to the base of neural spine in posterior trunk vertebrae.

29.Quadrangular coracoids

UNNAMED TAXON III (*Argentinosaurus huinculensis* + Unnamed taxon IV)

30. Presence of accesory spino-diapophyseal laminae in trunk vertebrae

UNNAMED TAXON IV (*Opisthocoelicaudia skarzynskii* and Titanosaurinae indet.- DGM "Serie B")

31. Absence of diapo-postzygapophyseal lamiane in posterior trunk vertebrae

UNNAMED TAXON V (*Aelosaurus* + Unnamed taxon VI)

32. Biconvex first caudal

33. Presence of dorsal prominence on inner face of scapula

UNNAMED TAXON VI (*Alamosaurus sanjuanensis* + Saltasaurinae)

34. Depressed mid- and posterior caudal centra with dorsoventrally convex lateral faces

35. Presence of pronounced lateral ridge on base of neural arch in mid-portion of tail

36. Relatively short posterior process of ischium.

SALTASAURINAE

37*. Short cervical prezygapophyses, with articular facets located near level of diapophyses.

38. Depressed anterior caudal centra, with dorsoventrally convex lateral faces
10(-). Antero-dorsal edge of neural spine palced posteriorly with respect to anterior root of mid-caudal postzygapophyses.

(-) reversal
(*) equivocal distribution

4. LIST OF TAXA CITED IN THE MORPHOLOGICAL COMPARISONS

Aelosaurus rionegrinus Powell, 1986 (Published 1987b)
Material:
MJG-R1 holotype
7 anterior caudal vertebrae
Incomplete left and right scapulae,
Left and right humeri,
Left and right radius and ulna (POWELL, 1987b, p.148)
5 metacarpals,
Right and left ischium (POWELL, 1987b, p. 148)
Right tibia
Right fibula,
1 astragalus
Some fragmentary bones

Angostura Colorada Formation
Campanian? Late Senonian (POWELL, 1987b)
Rio Negro Province

Additional material:
MACN-RN 147
caudal sequence of 15 partially articulated vertebrae (the last are amphicoelian, in contrast with the anterior procoelic ones)
Los Alamitos Formation

Collectors: R. Casamiquela, 1964; Bonaparte and Powell, and assistants, 1983

Comments: this species is of rather modest size, with the femur of about 1 m long. The robust humerus bears a prominent knob on the deltoid crest. The metacarpals are rather short and robust as in *Saltasaurus* (BONAPARTE, 1996: 104). POWELL (1987b) describes the aditional material (MACN-RN 147 - 15 caudal vertebrae). He gives, in page 148, the

description of the holotype MJG-R 1, including the diagnosis (as follows: "...Broad scapula with distal expanded end. Prominent and short ridge for muscular attachement near the upper border of the internal face of the scapula, as in *Saltasaurus loricatus*. Robust humerus with a prominent apex on the deltoid crest for insertion of the pectoral muscle. Short and robust metacarpals as in *Saltasaurus loricatus*. Pubis with broad but not bulky distal end, without ventral longitudinal elevation."; but he has not included any figure of the appendicular bones).

Aelosaurus sp. Salgado e Coria, 1993a
Material:
MPCA-27174:
5 caudal vertebrae, (lam.1,A,B,C p.125 + fig.2,3,4 p.120/121)
Right ulna, (not figured)
1 metacarpal, (lam.1,F p.125 + fig.7 p.123)
Left pubis, (lam.1,I p.125 + fig.8 p.123)
Right ischium (lam.1,H p.125 + fig.9 p.124)

MPCA-27175:
right ulna and radius (lam.1,D,E p.125 + fig.5,6 p. 122)

MPCA-27176/7: 2 dermal plates (lam.1,G p. 125)

Allen Formation - Inferior member
Campanian-Maastrichtian
Rio Negro Province - Salitral Moreno

Comments: The paper of SALGADO & CORIA (1993a) figures the appendicular elements, but there has been some confusion in the legends, as follows: figs. 5 and 6 indicate MPCA 27174, but text indicates that these bones should be from MPCA 27175. Furthermore, the radius depicted in fig. 6 is reversed (it shows a left radius, upside down). There is some error in the scale bar also, the ulna is smaller than the radius, but the text says that the smaller ulna (juvenile) conforms in size with the radius found, so the radius should be smaller than the ulna depicted.

Aelosaurus sp. Salgado, Coria & Calvo, 1997b
Material: MPCA-27100
4 anterior caudal vertebrae (fig.1, p. 45; fig.2, p.46)
2 incomplete sternal plates (fig.3,A, p.46)
Left humerus (fig.3,B, p.46)
2 metacarpals (fig.4, p.46),
Incomplete left femur (without proximal end) (fig.5,A, p.47)
Left tibia (fig.5,B, p.47)
Left fibula (fig.5,C, p.47)
4 left metatarsals (fig.7,8; p.48)
Left astragalus (fig. 6, p.47)

Los Alamitos Formation (middle section)
Campaniano
Rio Negro Province

Alamosaurus sanjuanensis Gilmore, 1922
Material:
USNM- 10486, holotype
Left scapula (GILMORE, 1946, fig.1 pl.10)

USNM-10487, paratype
Right ischium, incomplete (GILMORE, 1946, fig. 2, pl.10)

Ojo Alamo Formation
Upper Cretaceous
New Mexico
Collector: John B. Reeside Jr.
The bones pertain perhaps to two individuals (GILMORE, 1946, p.30)

Additional material:

USNM-15658 (Gilmore, 1946, p. 30; fig.3, pl.10)
Approximately the 21th caudal centrum and a caudal neural spine
Shale 3 to 8 feet above the base of Ojo Alamo Fm.
Barrel Springs Arroyo, 1 mile south of Ojo Alamo, New Mexico
Collector: John B.Reeside Jr., 1916

USNM-15560 (GILMORE, 1946)
30 articulated caudal vertebrae, beginning with the first
25 chevrons
2 ischia, right somewhat incomplete (p.39, fig.11,p.40)
Left scapula and coracoid (p.34, fig.6,p.35)
Right humerus (p. 36; fig.7A, fig.8 p.37)
Right ulna (p.37; fig.7A, p. 37; fig.9 p.38),
Right radius (p.37; fig.7A, p.37; fig.9 p.38),
Metacarpus (p.38; fig.10, p.38)
(humerus, radius, ulna and 5 metacarpals articulated)
2 sternal plates (p. 33; fig.5, p.34; pl.9)
Parts of 3 ribs

North Horn Formation (lower part)
Upper Cretaceous
Southwest toe of North Horn Mountain, Manti National Forest, Emery County, Utah
Collector: found by George B. Pearce, June, 15, 1937

Comments: this additional species of *Alamosaurus sanjuanensis* (USNM 15560) is considered the most important titanosaurid finding, not only for its completeness, but also because the material has been found articulated. The sacrum was not collected, and was observed in the field, and evidence was noted that the complete sacrum consisted of five vertebrae. This would contradict the normal titanosaurid sacral arrangement, with six vertebrae. Since the sacrum of *Alamosaurus* was left in the field, it is not possible to confirm this observation.

Andesaurus delgadoi Calvo e Bonaparte, 1991
Material: MUCPv 132, holotype.
Part of one individual with:
4 articulated posterior dorsal vertebrae
27 articulated caudal vertebrae in two sections (central anterior and central distal sections of the tail)
incomplete humerus (distal part – p. 307, fig. 8 A,B)
incomplete femur (without both ends – p. 307, fig. 7)
Ischia (left almost complete – p. 306, fig. 5, A, right incompl.) (see also CALVO, 1999, fig.7, p. 24)
Left pubis almost complete (p. 306, fig. 6, A (right), p.307) (see also CALVO, 1999, fig.7, p.24)
rib fragments

Rio Limay Formation
Albian-Cenomanian
Neuquén Proince
Collectors: Calvo and P. Puerta, 1987

Additional material: MUCPv-271 (Calvo, 1999: 22)
Partial pelvis (pubis in Calvo, 1999: 23, fig. 5)
Some caudal vertebrae
11 gastroliths
Collectors: found by Ruben Carolini in 1995 and collected by Calvo and assistants, 1996.

Comments: This species is referred to a family of its own - the Andesauridae. This family was regarded as a paraphyletic assemblage of primitive, non-titanosauridae sauropods (BONAPARTE, 1996). In the cladistic analysis of SALGADO *et al.* (1997a), *Andesaurus delgadoi* is positioned as the siter taxon of the Titanosauridae.
The additional material is discussed in the paper of CALVO (1999: 22/24). He gives pictures of the holotype (left pubis and ischium, fig.7, p. 24); and of the new specimen (right pubis fig.5, p.23)

Antarctosaurus brasiliensis Arid & Vizotto, 1971
Material: housed at Departamento de Geociências da Faculdade de Filosofia, Ciências e Letras de São José do Rio Preto.
GP-RD-2:
Left femur (distal middle portion) (Photos 1,2,3, p. 299)
GP-RD-3:
Right humerus (proximal middle portion) (Photos 4,5, p. 301)
GP-RD-4:
Dorsal vertebra (incomplete) (photos 6,7, p. 301)
Bauru Formation (Adamantina Formation ac. to BERTINI *et al.* 1993, p. 86).
Site: Km 5 of the São José do Rio Preto-Barretos state highway, State of São Paulo

Comments: "It is estimated that if the femur was complete is would have a length of about 1.55m, making it one of the largest sauropods in South America. However, the femur fragment lacks diagnostic features which would serve to identify this species, and the name

?A. brasiliensis is best regarded as a *nomen nudum"*. (Powell, 1986 *apud* BERTINI *et al.*, 1993: 86).

Antarctosaurus giganteus Huene, 1929
Material: MLP.23-316 holotype
2 incomplete caudal vertebrae
2 femora
Pubis (fragments)
Tibia (distal end)

Rio Neuquén Formation
Early Senonian
Neuquén Province
Collectors: Personnel of La Plata Museum

Comments: "The femora of this species are longer and slender than in *A. wichmannianus*, with little expanded proximal and distal articulation areas" (BONAPARTE, 1996: 108).

A. giganteus is depicted in the work of HUENE (1929) as follows:

Lam.35: fig. 10 left pubis (AC 2300)
Lam.36: fig.1 right femur; fig.2 left femur

Antarctosaurus wichmannianus Huene, 1929
Material: MACN 6904, holotype
Occipital and temporal regions of a skull, incomplete lower jaws
Left scapula
Right humerus (incomplete)
2 radii (incomplete)
Ulna (incomplete)
7 metacarpals
1 phalanx
Ilia (fragmentary)
Left and Right ischia (incomplete)
Pubis (fragment)
Left femur
Left tibia
Left fibula
5 metatarsals and phalanges

Rio Colorado Formation
Coniacian
Rio Negro Province
Collector: R. Wichmann, around 1916

Comments: This is a gigantic species. It has been traditionally classified in the subfamily Antarctosaurinae, *sensu* Powell,1986 by having "...Scapula with narrower blade than in Saltasaurinae and Argyrosaurinae. Ischium with narrow distal stem, somewhat wider distal. Pubic pedicel of ischium well developed, but short. Tibia with robust ends. Fibula with lateral

process made of two parallel tuberosities following the bone axis " (BONAPARTE, 1996: 107).

Antarctosaurus wichmannianus is depicted in HUENE (1929) as follows:
Cranium (lam. 28 and 29)
Vertebrae and ribs (lam. 30)
Distal part of a left ulna (lam. 30, fig. 6)
Left scapula (lam. 31, fig. 1)
Posterior half of the right ilium (lam. 31, fig. 2)
Right humerus (lam. 32, fig. 1)
Left ischium (lam. 32, fig. 2)
Distal part of fibula (lam. 32, fig. 4)
Left femur (lam. 33, fig. 1)
Left tibia (lam . 33, fig. 2)
Left fibula (lam. 33, fig. 3)
Metacarpals, metatarsals, astragalus and calcaneum (lam. 34)
Phalanges of manus and pes (lam. 35)

Antarctosaurus sp. Bonaparte & Bossi, 1967
Material: PVL-3670
Left premaxilla, a cervical and some caudal vertebrae,
Incomplete humerus,
Incomplete ulna and radius,
A small fragment of ilium,
Incomplete pubis and ischium,
Most of a femur (BONAPARTE, 1996, fig. 37,A,B), tibia and fibula (BONAPARTE, 1996, fig. 37,C).

Los Blanquitos Formation
Campanian?
Salta Province
Collectors: Bonaparte and assistants, 1966; Powell and assistants, 1982.

Comments: All pieces belong to one specimen. BONAPARTE, (1996: 104, text and fig. 37), considers it as a member of the Titanosaurinae, *sensu* Powell, based on charachters of the caudal vertebrae and elongate humerus. The material is discussed in POWELL (1979) and is there considered as *Laplatasaurus sp.* We have addopted the same view in the present work.

Argentinosaurus huinculensis Bonaparte & Coria, 1993
Material: PVPH-1, holotype
5 dorsal vertebrae
2 incomplete ribs
1 tibia (right, incomplete, with an eroded external face) – p. 278, fig. 8)
1 incomplete sacrum

Rio Limay Formation – Huincul Member
Albian-Cenomanian
Neuquén Province

Collectors: F. Romero and assistants, 1980; Bonaparte and Vince, and assistants, 1989.

Comments: BONAPARTE (1996) considered it as a member of the primitive, non titanosauridae family Andesauridae. In the cladistic analysis of SALGADO *et al.* (1997a), *A. huinculensis* is placed within the Titanosauridae.

Argyrosaurus superbus Lydekker, 1893
Material:
MLP.77-V-29-1, holotype
A complete left forelimb missing the phalanges.

Bajo Barreal Formation (possibly)
Early Senonian
Chubut Province
Collector: C. Ameghino, around 1900

Additional material:
PVL 4628
3 dorsal and 3 caudal vertebrae
Left scapula
Left humerus
Left and right radii and ulnae
Most of a right femur
Tibia (incomplete)
Rib fragments

Bajo Barreal Formation
Early Senonian
Chubut Province
Collectors: Bonaparte, Vince and Powell and assistants, 1982-1983

Comments: Powell, 1986 referred this additional specimen to the genus but with doubts to the same species (BONAPARTE, 1996: 109) "*Argyrosaurus*...bears several diagnostic characters... the heavy construction of the humerus, which in comparison with the incomplete one of *Antarctosaurus* is much heavier. The scapula of *Argyrosaurus* shows a differente angle between the longest axis of the blade and that of the acromial-glenoid expansion. Powell, 1986, emphasized the similarities of the forelimb of *Argyrosaurus* and that of *Alamosaurus*, although he recognized differences in the proportions of the metacarpals" (BONAPARTE, 1996: 109). It is classified within the Argyrosaurinae, *sensu* Powell, 1986: "Titanosaurids of great size, provided with robust limb bones, including metacarpals...pubis with wide, flat anterodorsal lamina, without distal thickenning" (BONAPARTE, 1996: 108).

Argyrosaurus superbus is depicted in HUENE (1929) as follows:

Lam.37: anterior left limb
Lam.38: left and right femora
Lam.39: vertebrae

The additional specimen, after POWELL (1986) is depicted in BONAPARTE (1996: 109, fig. 43), as follows:
Left scapula in lateral view (A)
Left humerus in anterior (B) and posterior (C) views
Left ulna in lateral view (D)
Right radius in lateral view (E)

Chubutisaurus insignis Corro, 1975
MACN 18222 holotype
Axial elements: 1 posterior dorsal centrum, 1 dorsal neural arch, 1a dorsal neural spine, 10 incomplete caudals

Appendicular elements:
left humerus
left radius
1 left ulna
left femur
left tibia
4 metacarpals

fragmentary remains

Cerro Barcino Formation (Or Gorro Frigio Formation, Cerro Barcino Member, Salgado, 1993)
Albian (possibly) or Aptian (SALGADO, 1993)
Chubut Province
Collectors: Corro and O.A. Gutiérrez, 1965

Comments: CORRO (1975) considered it a member of a new family - the Chubutisauridae. The paper of Corro only figures some of the vertebrae and gives a brief description of the femur and the humerus (including the dimensions). SALGADO (1993) makes comments on *Chubutisaurus* and redescribes the holotype. He describes the long bones in pages 266/267 and figures them in p. 269, fig 4, A (radius/ulna), B (humerus), C (femur), D (tibia), E-H, metacarpals. McINTOSH (1990) described briefly the radius, ulna and metacarpals, and considered it a member of the Brachiosauridae. In the cladistic analysis of SALGDO *et al.* (1997a), this species appears as the sister taxon of the Titanosauria.

Laplatasaurus araukanicus Huene, 1929
= *Titanosaurus araukanikus* (Powell, 1986)

Material:
MLP.CS.1128 – right tibia
MLP.CS.1127 – right fibula, lectotype
Hypodigm (each piece has a different number):
Cervical, dorsal and caudal vertebrae
Sternal plate
Right scapula
Coracoid
Left humerus (incomplete)

Left radius
Metacarpals
Left pubis
Metatarsals (incomplete)

Allen Formation
Campanian
Rio Negro Province
Collectors: S. Roth and R. Wichmann

Comments: Huene, 1929, proposed the species *Laplatasaurus araukanikus* based on part of the material. Powell, 1986, proposed the combination *Titanosaurus araukanikus*. The hypodigm probably represents more than one individual and the association of the different pieces is uncertain. This genus and species is characterized by long and slender limb bones. Considered a Titanosauridae, Titanosaurinae *sensu* Powell, 1986 (limb bones slender than in any other subfamily) (BONAPARTE, 1996)

Laplatasaurus araukanicus is depicted in HUENE (1929) as follows:
Lam. 22: vertebrae (fig.1/16) left sternal plate (fig.17) and young individual (fig.18/24, including apendicular skeleton)
Lam.23: scapulae and humeri
Lam.24:
Right ulna (Av.2081) de Rancho Ávila
Right radius (Av.2072) de Rancho Ávila
Left radius (locallity of Dr. Wichmann)
Lam.25: metacarpals I-V, phalanges and left pubis (CS 1059)
Lam.26: left and right ilia, right femur
Lam.27: left and right tibiae, right fibula

Laplatasaurus sp. Powell, 1979
(= *Antarctosaurus sp.* Bonaparte & Bossi, 1967)
Material: PVL.3670-1/14
Humerus (right, incomplete, PVL.3670-1, fig.3A,p.195)
Ulna (right, PVL.3670-2, fig.3B, p.195)
Radius (right, PVL.3670-3, fig.3C,D, p.195)
Femur (left, PVL.3670-4, fig.5A,B, p.197)
Tibia (right, PVL.3670-5, fig.5C, p.197)
Fibula (right/left(distal tird), PVL.3670-6/7, fig.5D,E, p.197)
Premaxila (PVL.3670-12, fig.2,p.194)
Ilium (fragmented) (left, PVL.3670-9, fig.4A, p.196)
Pubis (fragmented) (right, PVL.3670-10, fig.4C, p.196)
Ischium (fragmented) (left, PVL.3670-11?, fig.4B, p.196)
Cervical vertebra PVL.3670-13 – not figured)
Caudal vertebrae PVL.3670-14 – not figured)

Lirainosaurus astibiae Sanz *et al.*, 1999
Material:
Holotype: MCNA 7458 anterior caudal, probably 1th one. (MCNA = Museo de Ciencias Naturales de Alava)

Paratype:
Fragment of skull (MCNA 7439)
Isolated teeth (MCNA 7440/41)
9 dorsal vertebrae (MCNA 7442-50)
7 caudal vertebrae (MCNA 7451-57 + MCNA 1812)
Left scapula (MCNA 7459)
Right coracoid (MCNA 7460)
sternal plate (frag.) (MCNA 7461)
4 humeri (right and left, two sizes) (MCNA 7462-65)
Left Ilium (frag. – acetabular portion) (MCNA 7466)
Pubis (frag.) (MCNA 7467)
3 femora (MCNA 7468-right/70 + MCNA 3160)
Right Tibia (MCNA 7471)
Right Fibula (MCNA 7472)
2 dermal scutes (MCNA 7473/74)

Unnamed stratum (Upper part of unit B of Baceta et al. 1999; S3U1 unit of Astibia *et al.*, 1987, 1990 *apud* SANZ *et al.* 1999)
Upper Cretaceous (lower Maastrichitian or upper Campanian)
Lano Quarry, Condado de Trevino, (within Alava Province) Northcentral Spain.

The species is depicted as follows:

Vertebrae (plates 1-3)
Left and right humeri MCNA 7463 and 7462 (plate 4)
Left scapula MCNA 7459 (plate 4)
Right coracoid MCNA 7460 (plate 5)
Sternal plate MCNA 7461 (plate 5)
Left femur MCNA 7468 (plate 6)
Right tibia MCNA 7471 (plate 6)
Right fibula MCNA 7472 (plate 6)

Malawisaurus dixeyi (Haughton, 1928) comb.nov. JACOBS *et al.*, 1993
Material: Holotype – "The type is taken to be the anterior caudal vertebra illustrated by Haughton (1928) and catalogued as South African Museum nº 7405. The remaider of the material included by Haughton with the type (a right pubis, an incomplete scapula, and sternal plates) is considered topotypic" (JACOBS *et al.*, 1993: 525).

Additional material:
Premaxilla, dentary, teeth, cervial, dorsal and caudal vertebrae, sternal plates, ischium.
Upper member of the Early Cretaceous Dinosaur Beds (Lupata Group); Mwakasyunguti area, northern Malawi, Africa.

Comments: A rather confused taxon, it was former described as *Gigantosaurus dixeyi* Haughton, 1928, it was also identified as *Tornieria* by STROMER, 1932.

The girdle bones are depicted in JACOBS *et al.* (1993: 526) as follows:

Fig.1F: Nºs 89-123 and 89-124; articulated sternal plates, ventral view.
Fig.1G: MAL-142; left ischium, lateral view.

Opisthocoelicaudia skarzynskii Borsuk-Bialynicka, 1977
Material: ZPAL MgD-I/48 – holotype

11 presacral (dorsal) vertebrae
6 sacral vertebrae
34 caudals
11 pairs of thoracic ribs
Both sternal plates (fig.4,p.20; pl.11,fig.1)
Both scapulae and coracoids (fig.6,p.23; pl.7,fig.1)
Both humerus (fig.7,p.25; pl.8,fig.3; pl.9,fig.3a-d)
Both radius (fig.8,p.28; pl.7,fig.4,5; pl.11,fig.3)
Both ulnae (fig. 8, p. 28; pl.8,fig.5; pl.9,figl; pl.11,fig.3)
Metacarpals (right-I-III; left-I-V) (pl. 7,fig.3; pl.11,fig. 2)
Ilium (figs. 11,p.34; fig.12,p.35; pl.12, fig. 1ac)
Both pubes (fig.12,p.35;fig.13,p.36;pl.3,fig.6;pl.12,fig.1)
Both ischia (fig.12,p.35;fig.13,p.36;pl.3,fig.6;pl.12,fig.1b,c)
Both femur (left damaged) (fig.15,p.38; pl.fig.4, pl.13,figs.1,2)
Both tibiae (fig.16B,p.40; pl.11,fig.4;pl.13,fig.4;pl.14,figs.1,2)
Both fibulae (fig.16A,p.40; pl.11,fig.5;pl.13,fig.3;pl.14,fig.2,b,c)
Both astragalus (pl.14, fig.2)
Metatarsals (right-I-V; left-I,II,IV) (pl.14, fig.2-7)
Phalanges (incomplete number) (pl.13,fig.5-11; pl.14, fig.2ab)

Nemegt Formation, ?Upper Campanian or Lower Maastrichtian
Altan Ula IV, Nemegt Basin, Gobi Desert, Mongolia
Collector: Polish-Mongolian Palaeontological Expedition, 1965

Additional material (BORSUK-BIALYNICKA, 1977: 8):
ZPAL MgD-I/25c – A scapula and coracoid of a young individual. The coraco-scapular suture is unfused. The distal end of the scapula as well as a proximal part of its posterior border are damaged.

Comments: Only recently this species has been recognized as a member of the Titanosauridae (SALGADO *et al.*, 1997a). The identification was not made before because *Opisthocoelicaudia* bears aberrant morphological characters, not present in other members of the Titanosauridae. It has bifid dorsal spines (a trait present only in the Camarasauridae and the Diplodocidae), and lacks the most unequivocal titanosaurid feature – its anterior caudal vertebrae are not procoelic, as in all member of the family, being rather opisthocoelic. If *Opisthocoelicaudia* is in fact a member of the Titanosauridae, then it is the most important specimen, for its completeness (it lacks only the skull and neck vertebrae), and for the fact that the skeleton was found articulated.

Rocasaurus muniozi Salgado & Azpilicueta, 2000.
Material: MPCA-pv 46 – young individual
1 cervical centre
1 cervical neural arch

2 dorsal centra
3 dorsal neural archs
2 sacral neural archs
1 median caudal vertebra
1 mid-posterior caudal vertebra
2 isquia (fig. 9c, p. 264)
1 left pubis (fig. 9d, p. 264)
1 left ilium (fig. 9b, p. 264) + fragment of the right one
1 left femur (fig. 9a, p. 264)

Additional material:
MPCA-Pv 47,48,60: 3 anterior caudal centra
MPCA-Pv 49: 1 median caudal center
MPCA-Pv 50: 1 posterior caudal center
MPCA-Pv 51-56: 6 distal caudal centra
MPCA-Pv 57: 1 anterior caudal
MPCA-Pv 58: 1 median caudal
MPCA-Pv 59: 1 posterior caudal

Allen Formation (inferior member)
Maastrichtian or Campanian-Maastrichtian
Salitral Moreno, General Roca, Rio Negro Province, Patagonia Argentina.

Comments: this is a recently discovered and described titanosauridae. It was classified within the Saltasaurinae (SALGADO & AZPILICUETA, 2000).

Saltasaurus loricatus Bonaparte e Powell, 1980
Material:
PVL 4017-92 Holotype
A complete sacrum fused to both ilia

Hypodigm of 5 or more individuals (adult/subadult):

3 incomplete skulls,
1 axis, 14 cervicals, 20 dorsals, 3 sacra, 26 caudals,
4 scapulae, 3 coracoids, 4 sternal plates,
10 humeri,
5 ulnae, 4 radii,
5 metacarpals,
4 pubes, 2 ischia,
5 ilia,
5 femora,
5 tibiae, 4 fibulae,
7 metatarsals,
6 dermal scutes,
4 groups of associated (in natural position) dermal ossicles

Lecho Formation
Maastrichtian

Salta Province
Collectors: Bonaparte, Vince, Leal, Powell, assistants, 1976/77

Comments: this is the most complete Titanosauridae found in South America. The findings confirmed that at least some titanosaurids bore body armor. This species occupies a subfamily of its own – the Saltasaurinae. All pieces of the hypodigm were found associated. There is good description of the material in POWELL (1998). The material is depicted there as follows:

Right scapula PVL 4017-106 (fig. 28, p. 221)
Left coracoid PVL 4017-100 (fig. 29, p. 221)
Left sternal plate PVL 4017-102 (fig. 30, p. 222)
Left humerus PVL 4017-67 (fig. 31, p. 223)
Left ulna PVL 4017-74 (fig. 32, p. 223)
Left radius PVL 4017-78 (fig. 33, p. 224)
Right radius PVL 4017-76 (fig. 34, p. 224)
Right pubis PVL 4017-95 (fig. 35, p. 225)
Right ischium PVL 4017-99 (fig. 36, p. 225)
Right femur PVL 4017-79 (fig. 37, p. 226)
Right tibia PVL 4017-84/87 (fig. 38, 39 – juvenile, p.227)
Left fibula PVL 4017-85? (fig. 40, p.228)

Titanosaurus australis Lydekker, 1893
(= *Neuquensaurus australis* Powell, 1986)
Material: MLP Ly.1/2/3/4/5/6 Holotype
Caudal vertebrae

Hypodigm:
several groups of vertebrae indicated in detail by Powell, 1986
scapulae, coracoids,
humeri,
ulnae,
and most of postcranial bones from different localities.

Possibly from Rio Colorado and Allen Formations.
Coniacian and Campanian respectively
Neuquén and Rio Negro Provinces
Collectors: S. Roth (around 1891)
Personnel of La Plata Museum, around 1910-20.

Comments: "Both Lydekker and Huene used mixed specimens in their study of *Titanosaurus australis*. Powell, 1986, recognized some mixed pieces and tried to clarify the taxonomy of this species" (BONAPARTE, 1996: 105).
"Powell, 1986, stated that the material studied by Lydekker and by Huene and interpreted by them as *Titanosaurus* is actually a different genus, to which he named *Neuquensaurus*. The more significant differences between *Titanosaurus* and *Neuquensaurus* are in the morphology of the caudal vertebrae and in the bones of the forelimb. *Neuquensaurus* is, in turn, similar to *Saltasaurus*. The limb bones of *Neuquensaurus* are more slender than in *Saltasaurus*, the

scapula, although of some different outline, bears a similar medial projection on the anterior border as in *Saltasaurus*" (BONAPARTE, 1996: 106).

Since Powell has never published the results of his thesis, the use of the name *Neuquensaurus* is employed in an informal manner, for it is not validy. In the present work, we have chosen to use the name coigned by HUENE (1929): *Titanosaurus australis*

The material is depicted in HUENE (1929) as follows:
Lam.2 to 5, 7, 8: vertebrae
Lam.9: sternal plates, right and left scapulae, coracoids
Lam.10: right and left humerus
Lam.11:
Left ulna (CS 1058) fig.1
Right ulna (CS 1053) fig.2
Left ulna (CS 1306) fig.3
Left radius (CS 1175) fig.4
Left radius (CS 1176) fig.5
Left radius (CS 1174) fig.6
Right radius (CS 1172) fig.7
Rigth radius (CS 1169) fig.8
Lam.12: metacarpals II and IV, phalanges of manus and pes
Lam.13: ilium, pubis
Lam.14: right pubis, left ischium, left femur
Lam.15: left and right femora
Lam.16: right femur, left and right tibiae, right fibulae
Lam.17: right astragalus and calcaneus, metatarsals I,II,IV,V

Titanosaurus colberti Jain & Bandyopadhyay, 1997
Material: ISIR335/1-65, holotype - a partial skeleton, of one individual
9 cervicals (ISIR335/1-9)
7 dorsals (ISIR335/10-16)
14 ribs (ISIR335/17-30)
Complete sacrum with 6 co-ossified vertebrae and ribs (ISIR335/31)
16 caudals (ISIR335/32-47)
9 chevrons (ISIR335/48-56)
Left scapula (ISIR335/57)
Left coracoid (ISIR335/58)
Left humerus (ISIR335/59)
Left ulna (ISIR335/60)
Pair of ilia (ISIR335/61-62)
Pair of pubes (ISIR335/63-64)
Right ischium (ISIR335/65)

Lameta Formation of Wardha Valley, Dongarfaon village, Chandrapur district, Maharashtra, Central India.
Late Cretaceous (Maastrihtian)

Titanosaurus colberti is depicted in JAIN & BANDYOPADHYAY (1997) as follows.

Pectoral girdle (p. 121) (fig.16,I; fig. 18) (coracoid, fig.19)

Forelimb (p.121) Humerus (fig.20; fig.21,A,B), Ulna (fig.22; fig.21,C,D) (p.122/123)
Pelvic girdle (p. 124)
Ilium, Pubis (fig. 24; fig.21, E,F) (p. 124,125)
Ischium (fig. 25; fig. 21,I,J) (p. 125)

Comments: The paper of JAIN & BANDYOPADHYAY (1997) has an excellent overview of Indian titanosaurians, and extensive discussion of the taxa. It also includes a revised diagnosis of the genus *Titanosaurus* Lydekker, 1877.

Titanosaurus robustus Huene, 1929
(= *Neuquensaurus robustus* Powell, 1986)
Material: MLP.CS 1095/94, 1171, 1480 - lectotype
Right and left ulnae
Left radius
Left femur

Allen Formation (Campanian)
Rio Colorado Formation (Coniacian)
Rio Negro Province
Collectors: S. Roth, personnel of La Plata Museum, around 1895 to 1910.

Comments: "Huene (1929) proposed the species *T. robustus* based on the more robust condition of the limb bones of somes specimens of *Neuquensaurus*. Powell (1986) reviewed all this material and recognized the heavier condition of the bones interpretede by Huene as *T. robustus*, but was unable to detect anatomical differences supporting a specific distinction. Consequently, he considered *Neuquensaurus robustus* as a *nomen dubius*. It is possible that the heavier condition of the bones of *N. robustus* is the result of sexual dimorphism or individual variation of *N. australis*, bus this has not been demonstrated, yet" (BONAPARTE, 1996: 107).

Titanosaurus robustus is depicted in Huene, 1929 as follows:
Left sternal plate (CS 1295 lam.18, fig.1)
Right humerus (proximal half) (CS 1019, lam.18, fig.2)
Right ulna (CS 1095, lam.18, fig.3)
Left ulna (CS 1094, lam.18, fig.4)
Left radius (CS 1171) (lam.18, fig.5)
Right ilium (posterior half) (Av.2068, lam.18, fig.6)
Lam. 19:
left ilium (Av. 2069, figs.1,2)
right femur (CS 1125, fig.3)
left tibia (CS 2064, fig.4)
left fibula (CS 1265, fig.5)
Lam. 20:
left femur (CS 1480) fig.1
right tibia (CS 1303) fig.2
right fibula (Av. 2059) fig.3
Lam. 21: metatarsals I-V, phalanges

Since Powell has never published the results of his thesis (Powell, 1986), the use of the name *Neuquensaurus* is employed in an informal manner, for it is not validy. In the present work, we have chosen to use the name coigned by HUENE (1929): *Titanosaurus robustus*.

Titanosaurinae from Guararapes (SP) Leonardi & Duszczak, 1977
Left femur (distal end) (fig. 4, A,B,C,D; fig.5)
Left humerus (proximal end, very fragmented) (fig.2, A,B, fig.3)
Upper section of the "Bauru" Formation

Comments: the specimens belong to two different individuals and are too much incomplete for morphological comparisons. They are kept in a private collection of two farmers of "Fazenda Rio Preto" (LEONARDI & DUSZCZAK, 1977: 397).

CONCLUSÃO

Ao término do presente trabalho, chegamos às seguintes conclusões:

VARIAÇÃO MORFOLÓGICA DO MATERIAL ESTUDADO

Os ossos apendiculares de Peirópolis apresentam variação morfológica na maioria das categorias ósseas estudadas. Essa variação pôde ser separada em 2 (escápula, placas esternais, ulna, fêmur, fíbula), 3 (púbis, ísquio) ou 4 (rádios) morfótipos distintos. Os coracóides não foram separados em morfótipos, mesmo assim apresentam variação morfológica. O úmero e a tíbia apresentam uma única morfologia, o que foi interpretado como não existência de mais de um morfótipo nessas categorias, ou simplesmente o resultado da limitação da amostra.

Entre as categorias que foram separadas em 3 ou mais morfótipos, duas delas eram morfologicamente semelhantes, e as demais bastante diferentes dessas duas.

A evidência morfológica sugere que a amostra é composta ou por três espécies distintas ou por duas espécies e uma forma variante (talvez relacionada ao dimorfismo sexual) pertencente a uma delas.

DIVERSIDADE FAUNÍSTICA ENTRE O TRÊS SÍTIOS FOSSILÍFEROS

O estudo mostrou que não existe um conjunto de morfótipos que seja exclusivo de um único sítio fossilífero. Em Serra da Galga e Localidade 1 há uma mistura de pelo menos dois morfótipos, para alguns tipos de ossos. O sítio Rodovia não apresenta mistura de morfótipos, mas os restos provenientes de lá são escassos. Além disso, os morfótipos presentes na amostra de Rodovia também estão presentes em pelo menos um dos outros dois sítios.

Localidade 1 produziu a maior quantidade de ossos (incluindo séries vertebrais articuladas e duas pelves). É o único sítio representado por um mapa de campo. O mapa indica claramente a presença de mais de um indivíduo nessa amostra. Os ossos de menor tamanho foram encontrados nesse sítio, indicando a presença de indivíduos jovens.

Os outros dois sítio também são compostos por uma mistura de indivíduos, o que se comprova pela presença de ossos de um mesmo lado do corpo (direito ou esquerdo), ou ossos de diferentes tamanhos (indicando indivíduos de diferentes idades).

Portanto, todos os três sitios representam parte da população original, e não estão relacionados a nenhuma fauna específica própria.

PRESENÇA DE SINAPOMORFIAS

De um total de 42 sinapomorfias possíveis relacionadas exclusivamente aos ossos apendiculares, 33 estão presentes no material de Peirópolis. A presenças destas sinapomorfias permitiram diagnosticar o material de Peirópolis como Sauropoda, Titanosauria, Titanosauridae (não-Saltasaurinae)

CARACTERÍSTICAS MORFOLÓGICAS DO MATERIAL BRASILEIRO

Os ossos de Peirópolis apresentam características morfológicas similares e únicas em relação a outras espécies de titanossaurídeos de diferentes partes do mundo, especialmente em relação ao gênero *Aelosaurus*, da Argentina.

Entre as caracteristicas próprias do material brasileiro, podemos citar: expansões na borda superior distal da lâmina escapular; protuberância anterior do coracóide MCT 1691-R; perfil anterior triangular das placas esternais do morfótipo 1; presença de um processo látero-anterior em todas as placas esternais (compartilhada apenas com *Lirainosaurus astibiae*); elevação sobre a crista delto-peitoral do úmero (compartilhada apenas com *Aelosaurus*); escavação distal nas ulnas do morfótipo 1; desnível na margem anterior, abaixo da inserção do músculo ambiens nos púbis do morfótipo 2; reentrância sob a lâmina isquiádica em isquios do morfótipo 1; elevação oblíqua medial das fibulas do morfótipo 2.

LEVANTAMENTO DA VARIAÇÃO MORFOLÓGICA

O presente trabalho sugeriu que os ossos apendiculares apresentam variação morfológica que pode ser a fonte para definição de novos caracteres, os quais poderão ser potencialmente úteis na elaboração de novas hipóteses filogenéticas tendo em vista a familia Titanosauridae.

PERSPECTIVAS PARA O FUTURO

O presente trabalho foi apenas uma descrição preliminar de alguns materiais que compõem a coleção de dinossauros do Departamento Nacional de Produção Mineral (Rio de Janeiro). Ainda há muitos ossos fossilizados no aguardo de serem catalogados e estudados. Entre eles, há uma conjunto de cerca de 30 metapodiais, incluindo metacarpais, metatarsais e astrágalos. Há também um grande número de vértebras (principalmente caudais, mas também dorsais e cervicais). Todos esses materiais continuam inéditos para a ciência. Além desses, as três séries vertebrais descritas por POWELL (1987a – séries "A", "B" e "C"), deveriam ser redescritas detalhadamente, e sofrer uma revisão, com enfoque das novas teorias filogenéticas.

Tudo isso é apenas uma amostra do que significa o problema representado pelos Titanossaurídeos do Brasil. Esperamos encontrar futuros dados de campo que ajudarão a identificar materiais procedentes dos três jazigos principais explorados por Price, dando continuidade ao trabalho desse importante paleontólogo brasileiro.

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